Ernst Mayr Library, MCZ
MCZ 1FZ0

WIL
8424
.a

HARVARD UNIVERSITY

Library of the
Museum of
Comparative Zoology

The Wilson Bulletin

PUBLISHED BY THE WILSON ORNITHOLOGICAL SOCIETY

VOLUME 93 1981 QUARTERLY

EDITOR: JON C. BARLOW
REVIEW EDITOR: ROBERT RAIKOW
COLOR PLATE EDITOR: WILLIAM A. LUNK
ASSISTANT EDITOR: MARGARET L. MAY
SENIOR EDITORIAL ASSISTANTS: GARY BORTOLOTTI
NANCY FLOOD
EDITORIAL ASSISTANTS: C. DAVISON ANKNEY
KEITH L. BILDSTEIN
JAMES D. RISING
RICHARD R. SNELL

President—Abbot S. Gaunt, Department of Zoology, Ohio State University, Columbus, Ohio 43210.

First Vice-President—Jerome A. Jackson, Department of Biological Sciences, P.O. Drawer Z, Mississippi State University, Mississippi State, Mississippi 39762.

Second Vice-President—Clait E. Braun, Wildlife Research Center, 317 West Prospect St., Fort Collins, Colorado 80526.

Editor—Jon C. Barlow, Department of Ornithology, Royal Ontario Museum, 100 Queen's Park, Toronto, Ontario, Canada M5S 2C6.

Secretary—Curtis S. Adkisson, Department of Biology, Virginia Polytechnic Institute and State University, Blacksburg, Virginia 24061.

Treasurer—Robert D. Burns, Department of Biology, Kenyon College, Gambier, Ohio 43022.

Elected Council Members—Richard C. Banks (term expires 1982); Mary H. Clench (term expires 1983); Helen Lapham (term expires 1984).

DATES OF ISSUE OF VOLUME 93
OF THE WILSON BULLETIN

NO. 1—14 MAY 1981
NO. 2—20 AUGUST 1981
NO. 3—29 OCTOBER 1981
NO. 4—22 FEBRUARY 1982

CONTENTS OF VOLUME 93

NUMBER 1

OBSERVATIONS OF SEABIRDS DURING A CRUISE FROM ROSS ISLAND TO ANVERS ISLAND, ANTARCTICA ---- *Robert M. Zink* 1

DISPLAY BEHAVIOR OF OVENBIRDS (*Seiurus aurocapillus*) II. SONG VARIATION AND SINGING BEHAVIOR ---- *M. Ross Lein* 21

THE MAYFIELD METHOD OF ESTIMATING NESTING SUCCESS: A MODEL, ESTIMATORS AND SIMULATION RESULTS ---- *Gary L. Hensler and James D. Nichols* 42

NARROWLY DISJUNCT ALLOPATRY BETWEEN BLACK-CAPPED AND CAROLINA CHICKADEES IN NORTHERN INDIANA ---- *Peter G. Merritt* 54

TOE FUSION IN OSCINES ---- *George A. Clark, Jr.* 67

ENVIRONMENTAL EFFECTS ON ROOSTING BEHAVIOR OF CHIMNEY SWIFTS *Richard M. Zammuto and Edwin C. Franks* 77

GENERAL NOTES

OBSERVATION OF A BROOD OF SHARP-SHINNED HAWKS IN ONTARIO, WITH COMMENTS ON THE FUNCTIONS OF SEXUAL DIMORPHISM *Helmut C. Mueller, Nancy S. Mueller and Patricia G. Parker* 85

FOOD DEPRIVATION AND TEMPERATURE REGULATION IN NESTLING FERRUGINOUS HAWKS *Diana F. Tomback and Joseph R. Murphy* 92

AERIAL "PLAY" OF BLACK VULTURES ---- *Walter A. Thurber* 97

THE SHOULDER-SPOT DISPLAY IN RUFFED GROUSE ---- *Allan Garbutt* 98

THE AGONISTIC REPERTOIRE OF SANDHILL CRANES *Stephen A. Nesbitt and George W. Archibald* 99

NOTES ON THE SLENDER ANTBIRD ---- *Edwin O. Willis and Yoshika Oniki* 103

NOTES ON THE UNIFORM CRAKE IN COSTA RICA ---- *F. G. Stiles* 107

TRICHOMONIASIS IN BALD EAGLES ---- *Ward B. Stone and Peter E. Nye* 109

Protocalliphora INFESTATION IN BROAD-WINGED HAWKS *Scott Crocoll and James W. Parker* 110

HERRING GULL ATTACKS AND EATS ADULT MALE OLDSQUAW ---- *Richard R. Snell* 110

RED-LEGGED KITTIWAKES FORAGE IN MIXED-SPECIES FLOCKS IN SOUTHEASTERN ALASKA ---- *Douglas Siegel-Caúsey and Thomas E. Meehan* 111

GROUND-FEEDING METHODS AND NICHE SEPARATION IN THRUSHES ---- *Alan Tye* 112

AMERICAN COOT DISTRIBUTION AND MIGRATION IN COLORADO *Warner P. Gorenzel, Ronald A. Ryder and Clait E. Braun* 115

REPRODUCTIVE RATE AND RENESTING OF RED-WINGED BLACKBIRDS IN MINNESOTA *Daniel W. Moulton* 119

MIGRATION SPEEDS OF THREE WATERFOWL SPECIES *Frank C. Bellrose and Robert C. Crompton* 121

ORNITHOLOGICAL LITERATURE ---- 125

ORNITHOLOGICAL NEWS ---- 135

NUMBER 2

THE RUFOUS-FACED CRAKE (*LATERALLUS XENOPTERUS*) AND ITS PARAGUAYAN CONGENERS
Robert W. Storer 137

RESOURCE USE STRATEGIES OF WADING BIRDS ---- *James A. Kushlan* 145

AGE RATIOS AND THEIR POSSIBLE USE IN DETERMINING AUTUMN ROUTES OF PASSERINE MIGRANTS ---- *C. John Ralph* 164

WEATHER, MIGRATION AND AUTUMN BIRD KILLS AT A NORTH FLORIDA TV TOWER
Robert L. Crawford 189

CLIMATIC INFLUENCES ON PRODUCTIVITY IN THE HOUSE SPARROW ---- *W. Bruce McGillivray* 196

CANADA GOOSE BROOD BEHAVIOR AND SURVIVAL ESTIMATES AT CREX MEADOWS, WISCONSIN
Michael C. Zicus 207

BREEDING BIRD POPULATIONS IN THE GREAT SMOKY MOUNTAINS, TENNESSEE AND NORTH CAROLINA ---- *S. Charles Kendeigh and Ben J. Fawver* 218

NEST-SITE SELECTION AMONG ADÉLIE, CHINSTRAP AND GENTOO PENGUINS IN MIXED SPECIES ROOKERIES ---- *Nicholas J. Volkman and Wayne Trivelpiece* 243

COWBIRD PARASITISM AND EVOLUTION OF ANTI-PARASITE STRATEGIES IN THE YELLOW WARBLER ---- *Karen L. Clark and Raleigh J. Robertson* 249

INTERACTIVE BEHAVIOR AMONG BALD EAGLES WINTERING IN NORTH-CENTRAL MISSOURI
Curtice R. Griffin 259

PRESIDENT'S MESSAGE ---- 264

GENERAL NOTES

INTERSPECIFIC SONG MIMESIS BY A LINCOLN SPARROW
Luis F. Baptista, Martin L. Morton and Maria E. Pereyra 265

NOTES ON PURPLE GALLINULES IN COLOMBIAN RICEFIELDS ---- *Wallace D. McKay* 267

AGONISTIC BEHAVIOR OF THE WHITE-BREASTED NUTHATCH ---- *Lawrence Kilham* 271

EVASIVE BEHAVIOR OF AMERICAN COOTS TO KLEPTOPARASITISM BY WATERFOWL
Mark R. Ryan 274

ADDITIONAL EVIDENCE OF EGG-MOVING BEHAVIOR BY FEMALE GADWALLS
Robert J. Blohm 276

MALLARD USING MOVING VEHICLES FOR PREDATOR AVOIDANCE
Bruce C. Thompson and James E. Tabor 277

OCHRACEOUS WREN FAILS TO RESPOND TO MOBBING CALLS IN A HETEROSPECIFIC FLOCK
William H. Buskirk 278

FISH ATTACK ON BLACK GUILLEMOT AND COMMON EIDER IN MAINE *Thomas W. French* 279

CROWS STEAL GOLF BALLS IN BANGLADESH ---- *Richard M. Poché* 280

NOTES ON THE STATUS OF THE COMMON AFRICAN WAXBILL IN AMAZONIA
David C. Oren and Nigel J. H. Smith 281

DISTRIBUTION AND REPRODUCTIVE SUCCESS OF ZONE-TAILED HAWKS IN WEST TEXAS
Sumner W. Matteson and John O. Riley 282

THREE CRESTED EAGLE RECORDS FOR GUATEMALA
David H. Ellis and Wayne H. Whaley 284

ORNITHOLOGICAL LITERATURE ---- 286

NUMBER 3

SUBSPECIES VS FORGOTTEN SPECIES: THE CASE OF GRAYSON'S ROBIN (*Turdus graysoni*)
Allan R. Phillips 301

HYPERPHAGIA AND SOCIAL BEHAVIOR OF CANADA GEESE PRIOR TO SPRING MIGRATION
M. Robert McLandress and Dennis G. Raveling 310

A MULTIPLE SENSOR SYSTEM FOR MONITORING AVIAN NESTING BEHAVIOR
James A. Cooper and Alan D. Afton 325

FORAGING SPEEDS OF WARBLERS IN LARGE POPULATIONS AND IN ISOLATION
Douglass H. Morse 334

DIFFERENTIAL PASSERINE DENSITY AND DIVERSITY BETWEEN NEWFOUNDLAND AND OFFSHORE GULL ISLAND ---- *Monique I. Vassallo and Jake C. Rice* 340

ENVIRONMENTAL INFLUENCE ON SOARING IN WINTERING RED-TAILED HAWKS
Charles R. Preston 350

BREEDING SUCCESS IN AN ISOLATED POPULATION OF ROCK DOVES
David E. Preble and Frank H. Heppner 357

RELATIVE ABUNDANCE OF GEORGIA CAPRIMULGIDS BASED ON CALL-COUNTS
Robert J. Cooper 363

NON-DRUMMING MALES IN A RUFFED GROUSE POPULATION ---- *Gordon W. Gullion* 372

GENERAL NOTES

BEHAVIORAL IMPLICATIONS OF ABERRANT SONG OF A RED-EYED VIREO
Jake C. Rice 383

COURTSHIP FEEDING AND COPULATION OF ROYAL TERNS ---- *Lawrence Kilham* 390

TWO CASES OF COMMENSAL FEEDING BETWEEN PASSERINES ---- *Mark B. Robbins* 391

FOOD FINDING IN BLACK-CAPPED CHICKADEES: ALTRUISTIC COMMUNICATION?
Millicent S. Ficken 393

THE SENTINEL CROW AS AN EXTENSION OF PARENTAL CARE
Gloria M. D'Agostino, Lorraine E. Giovinazzo and Stephen W. Eaton 394

BEHAVIOR OF A MALE LEAST BITTERN INCUBATING AFTER LOSS OF MATE
B. T. Aniśkowicz 395

NOTES ON BROWN PELICANS IN PUERTO RICO
Ralph W. Schreiber, David W. Belitsky and Bruce A. Sorrie 397

EGGS OF THE MARBLED MURRELET ---- *Lloyd F. Kiff* 400

FIRST DOCUMENTED CINNAMON TEAL NESTING IN NORTH DAKOTA PRODUCED HYBRIDS
John T. Lokemoen and David E. Sharp 403

FIRST RECORD OF THE BLACK-CHINNED HUMMINGBIRD IN ALBERTA
Philip H. R. Stepney and Peter C. Boxall 405

ORNITHOLOGICAL LITERATURE ---- 407

REPORT OF THE CONSERVATION COMMITTEE—1980 ---- 438

NUMBER 4

ON AERIAL AND GROUND DISPLAYS OF THE WORLD'S SNIPES ---------- *George Miksch Sutton* 457

FORAGING OF FIVE BIRD SPECIES IN TWO FORESTS WITH DIFFERENT VEGETATION STRUCTURE
Brian A. Maurer and Robert C. Whitmore 478

AGE AND SEX DIFFERENCES IN WING LOADING AND OTHER AERODYNAMIC CHARACTERISTICS OF SHARP-SHINNED HAWKS ------ *Helmut C. Mueller, Daniel D. Berger and George Allez* 491

EVIDENCE FOR AERODYNAMIC ADVANTAGES OF TAIL KEELING IN THE COMMON GRACKLE
Scott Hickman 500

REPRODUCTIVE CORRELATES OF ENVIRONMENTAL VARIATION AND NICHE EXPANSION IN THE CAVE SWALLOW IN TEXAS ---------- *Robert F. Martin* 506

HORNED LARK BREEDING BIOLOGY AT CAPE ST. MARY'S, NEWFOUNDLAND
Richard J. Cannings and William Threlfall 519

ASPECTS OF THE BREEDING BIOLOGY OF A SUBTROPICAL ORIOLE, *Icterus gularis*
Barbara Yohai Pleasants 531

GENERAL NOTES

AN EXAMPLE OF A HYBRID GREEN JAY × BLUE JAY
Warren M. Pulich and Rebecca M. Dellinger 538

DUSKY SEASIDE SPARROW FEEDS RED-WINGED BLACKBIRD FLEDGLINGS
James L. Rakestraw and James L. Baker 540

STATISTICAL SIGNIFICANCE AND DENSITY-DEPENDENT NEST PREDATION
Stephen D. Fretwell and Frank S. Shipley 541

A COMPARISON OF NEST-SITE AND PERCH-SITE VEGETATION STRUCTURE FOR SEVEN SPECIES OF WARBLERS ---------- *Scott L. Collins* 542

USE OF ARTIFICIAL PERCHES ON BURNED AND UNBURNED TALLGRASS PRAIRIE
Janet Jean Knodel-Montz 547

JUVENILE PEREGRINE FALCON SWOOPS ON ROSEATE SPOONBILLS ---------- *E. Scott Clark* 548

SYMBIOTIC INTERACTION BETWEEN STARLINGS AND DEER ---------- *Robert K. Murphy* 549

CATTLE EGRETS FEEDING IN ASSOCIATION WITH HUMAN WORKERS -------- *G. K. Menon* 549

SCRUB JAY CAPTURES HERMIT THRUSH IN FLIGHT
M. Robert McLandress and Ilse McLandress 550

FOOD HABITS OF BLACK-BELLIED WHISTLING DUCKS OCCUPYING RICE CULTURE HABITATS ---------- *Godfrey R. Bourne* 551

HOUSE SPARROWS FLUSHING PREY FROM TREES AND SHRUBS
Harland D. Guillory and Jack H. Deshotels 554

DIFFERENTIAL PREDATION BY TWO SPECIES OF PISCIVOROUS BIRDS
Fritz L. Knopf and Joseph L. Kennedy 554

RED PHALAROPE EATING CARRION ---------- *Wade Wander* 557

RE-MATING OF A LESSER SNOW GOOSE
Kenneth F. Abraham, Pierre Mineau and Fred Cooke 557

COMMON EIDER PLAYS "POSSUM" ---------- *Douglas B. McNair* 559

TERRITORIAL ATTACHMENT AND MATE FIDELITY BY HORNED GREBES
Robert S. Ferguson 560

EFFECTS OF REDHEAD NEST PARASITISM ON MALLARDS
Larry G. Talent, Gary L. Krapu and Robert L. Jarvis 562

SURVIVAL OF A DEMAXILLATE RED-WINGED BLACKBIRD ---------- *Kent L. Fiala* 563

MINIMIZING INVESTIGATOR DISTURBANCE IN OBSERVATIONAL STUDIES OF COLONIAL BIRDS: ACCESS TO BLINDS THROUGH TUNNELS
Gary W. Shugart, Mary A. Fitch and Vern M. Shugart 565

ORNITHOLOGICAL LITERATURE ---------- 570

PROCEEDINGS OF THE SIXTY-SECOND ANNUAL MEETING ---------- 575

INDEX ---------- 589

WIL
8424
.a

COMP. ZOOL.
LIBRARY
MAY 26 1981
HARVARD

The Wilson Bulletin

PUBLISHED BY THE WILSON ORNITHOLOGICAL SOCIETY

VOL. 93, NO. 1 MARCH 1981 PAGES 1–136

THE WILSON ORNITHOLOGICAL SOCIETY

FOUNDED DECEMBER 3, 1888

Named after ALEXANDER WILSON, the first American Ornithologist.

President—George A. Hall, Department of Chemistry, West Virginia University, Morgantown, West Virginia 26506.

First Vice-President—Abbot S. Gaunt, Department of Zoology, Ohio State University, Columbus, Ohio 43210.

Second Vice-President—Jerome A. Jackson, Department of Biological Sciences, P.O. Drawer Z, Mississippi State University, Mississippi State, Mississippi 39762.

Editor—Jon C. Barlow, Department of Ornithology, Royal Ontario Museum, 100 Queen's Park, Toronto, Ontario, Canada M5S 2C6.

Secretary—Curtis S. Adkisson, Department of Biology, Virginia Polytechnic Institute and State University, Blacksburg, Virginia 24061.

Treasurer—Robert D. Burns, Department of Biology, Kenyon College, Gambier, Ohio 43022.

Elected Council Members—Sidney A. Gauthreaux, Jr. (term expires 1981); Richard C. Banks (term expires 1982); Mary H. Clench (term expires 1983).

Membership dues per calendar year are: Active, $16.00; Student, $14.00; Sustaining, $25.00; Life memberships $250 (payable in four installments).

THE WILSON BULLETIN is sent to all members not in arrears for dues.

THE JOSSELYN VAN TYNE MEMORIAL LIBRARY

The Josselyn Van Tyne Memorial Library of the Wilson Ornithological Society, housed in the University of Michigan Museum of Zoology, was established in concurrence with the University of Michigan in 1930. Until 1947 the Library was maintained entirely by gifts and bequests of books, reprints, and ornithological magazines from members and friends of the Society. Now two members have generously established a fund for the purchase of new books; members and friends are invited to maintain the fund by regular contribution, thus making available to all Society members the more important new books on ornithology and related subjects. The fund will be administered by the Library Committee, which will be happy to receive suggestions on the choice of new books to be added to the Library. William A. Lunk, University Museums, University of Michigan, is Chairman of the Committee. The Library currently receives 195 periodicals as gifts and in exchange for *The Wilson Bulletin*. With the usual exception of rare books, any item in the Library may be borrowed by members of the Society and will be sent prepaid (by the University of Michigan) to any address in the United States, its possessions, or Canada. Return postage is paid by the borrower. Inquiries and requests by borrowers, as well as gifts of books, pamphlets, reprints, and magazines, should be addressed to: The Josselyn Van Tyne Memorial Library, University of Michigan Museum of Zoology, Ann Arbor, Michigan 48109. Contributions to the New Book Fund should be sent to the Treasurer (small sums in stamps are acceptable). A complete index of the Library's holdings was printed in the September 1952 issue of *The Wilson Bulletin* and newly acquired books are listed periodically. A list of currently received periodicals was published in the December 1978 issue.

THE WILSON BULLETIN
(ISSN 0043-5643)

The official organ of the Wilson Ornithological Society, published quarterly, in March, June, September, and December. The subscription price, both in the United States and esewhere, is $20.00 per year. Single copies, $4.00. Subscriptions, changes of address and claims for undelivered copies should be sent to the Treasurer. Most back issues of the *Bulletin* are available and may be ordered from the Treasurer. Special prices will be quoted for quantity orders.

All articles and communications for publications, books and publications for reviews should be addressed to the Editor. Exchanges should be addressed to The Joselyn Van Tyne Memorial Library, Museum of Zoology, Ann Arbor, Michigan 48109. Known office of publication: Department of Zoology, Ohio State University, 1827 Neil Avenue, Columbus, Ohio 43210.

Second class postage paid at Columbus, Ohio and at additional mailing office.

© Copyright 1981 by the Wilson Ornithological Society

Printed by Allen Press, Inc., Lawrence, Kansas 66044, U.S.A.

Antarctic Petrel *(Thalassoica antarctica)*. Amundsen Sea, Antarctica, January 1980. Photograph by J.R. Jehl, Jr.

THE WILSON BULLETIN

A QUARTERLY MAGAZINE OF ORNITHOLOGY

Published by the Wilson Ornithological Society

VOL. 93, NO. 1 MARCH 1981 PAGES 1–136

Wilson Bull., 93(1), 1981, pp. 1–20

OBSERVATIONS OF SEABIRDS DURING A CRUISE FROM ROSS ISLAND TO ANVERS ISLAND, ANTARCTICA

ROBERT M. ZINK

The breeding avifauna of the Sub-Antarctic and Antarctic consists of about 65 species, mostly seabirds. In the antarctic region, which includes the Antarctic continent, Peninsula and adjacent islands, there are 18 breeding species; 8 are restricted as breeders to the Antarctic Peninsula (Watson 1975). These 18 species depend largely on the sea for their existence and most are highly pelagic, only coming to land for breeding during the short austral summer. Sub-adult and foraging adult seabirds from subantarctic islands and the wintering Arctic Tern (*Sterna paradisaea*) are also found in antarctic waters during the austral summer. During the austral spring, under the influence of warming temperatures, wind and water currents, the continuous band of ice which surrounds the Antarctic continent and much of the Peninsula in winter, breaks up into pack ice and open water. Seabirds forage in continuous daylight of the austral summer and exploit plankton-abundant regions of the antarctic oceans.

Most information available on antarctic and subantarctic seabirds has resulted from terrestrial studies of their breeding biology. Although little is known about their pelagic distributions, behaviors and ecologies (Watson 1975, Ainley et al. 1978), these are influenced by prolonged sexual immaturity, nonbreeding periods when sexually mature, absence between bouts of incubation and foraging for food for young. In addition, there is little known about patterns in pelagic seabird community composition and species interactions. Biotic and abiotic determinants of species occurrences are also poorly understood (Watson 1975) although data exist on effects of sea water temperature (Szijj 1967), ice concentration (Cline et

al. 1969, Zink 1978, Ainley et al. 1978) and local plankton blooms (Cline et al. 1969, Ainley et al. 1978) on bird distributions.

Early studies (Gain 1914; Siple and Lindsey 1937; Holgerson 1945, 1957; Bierman and Voous 1950) established the broad patterns of seabird distributions and general pelagic ecology in Antarctica; recent summaries of many aspects of antarctic avian biology can be found in Watson et al. (1971) and Watson (1975). In addition, Watson (1975) provides a useful discussion of the maritime and terrestrial physical environments.

This study contributes information on the pelagic distribution, abundance and habits of 16 species of seabirds obtained during an austral summer cruise aboard the USCGC Glacier, while it traveled through the Ross, Amundsen and Bellingshausen seas, from McMurdo Station (Ross Island) to Palmer Station (Anvers Island). Recent seabird observations from the areas covered herein include those of Erickson et al. (1972) and Darby (1970), and are compared with recent pelagic seabird surveys from the Weddell Sea (Cline et al. 1969, Parmelee 1977, Zink 1978).

ITINERARY AND METHODS

The route and itinerary of the Glacier are shown in Fig. 1. This study was largely opportunistic as the purpose of this portion of the 1976 International Weddell Sea Oceanographic Expedition (IWSOE) was merely to reach Palmer Station, consequently, the route depended mostly on pack ice densities. Of the 136.1 h of observation, 99.1 h were taken in the Ross Sea (170°E–135°W), 23.5 h in the Amundsen Sea (135°W–90°W) and 13.5 h were mostly in ice-free portions of the Bellingshausen Sea (90°W–66°W).

Observations were made from the "flying bridge" of the Glacier, 16 m above the waterline, during periods of various lengths (0.5–4.5 h) throughout the day. A minute by minute account (in GMT) was kept of numbers and behavior of birds and seals sighted within approximately 0.4 km of each side of the ship, providing a census strip width of 0.8 km. The data on seals are discussed elsewhere (in prep.). To determine the transect boundaries a 12.7 × 38.1 cm rectangular board with a line, describing an angle of 2.3°, drawn diagonally from a top corner to a point on the opposite 12.7 cm side was used. While the top (i.e., 38.1 cm) edge of the board was sighted to the horizon (and perpendicular to the ship's course), a simultaneous sighting was taken along the line, which intersected the water 0.4 km from the observer (for details see Cline et al. [1969]). I tried to monitor specific birds following the ship to prevent multiple entries of given individuals. When several individuals of the same species were following the ship, all individuals seen at 5–10 min intervals were counted and the approximate turn-over rate was estimated. Maximum number in sight during any count and turnover rate were used to estimate the number of a given species seen during the transect period. Estimated numbers of birds in large flocks were probably conservative; direct counts of flocks while the Glacier was stuck in pack ice showed that initial estimates were low by as much as 30–40%.

Pack ice concentration during each observation period was recorded in oktas (0 indicating open seas, 8 representing solid pack). Ice concentrations changed rapidly during many censuses and prevented a precise correlation of each sighting with a specific okta value (see discussion of Adélie Penguin [*Pygoscelis adeliae*] for an example). Also, the okta value assigned to a flying bird or one foraging in a relatively narrow zone of several ice concentra-

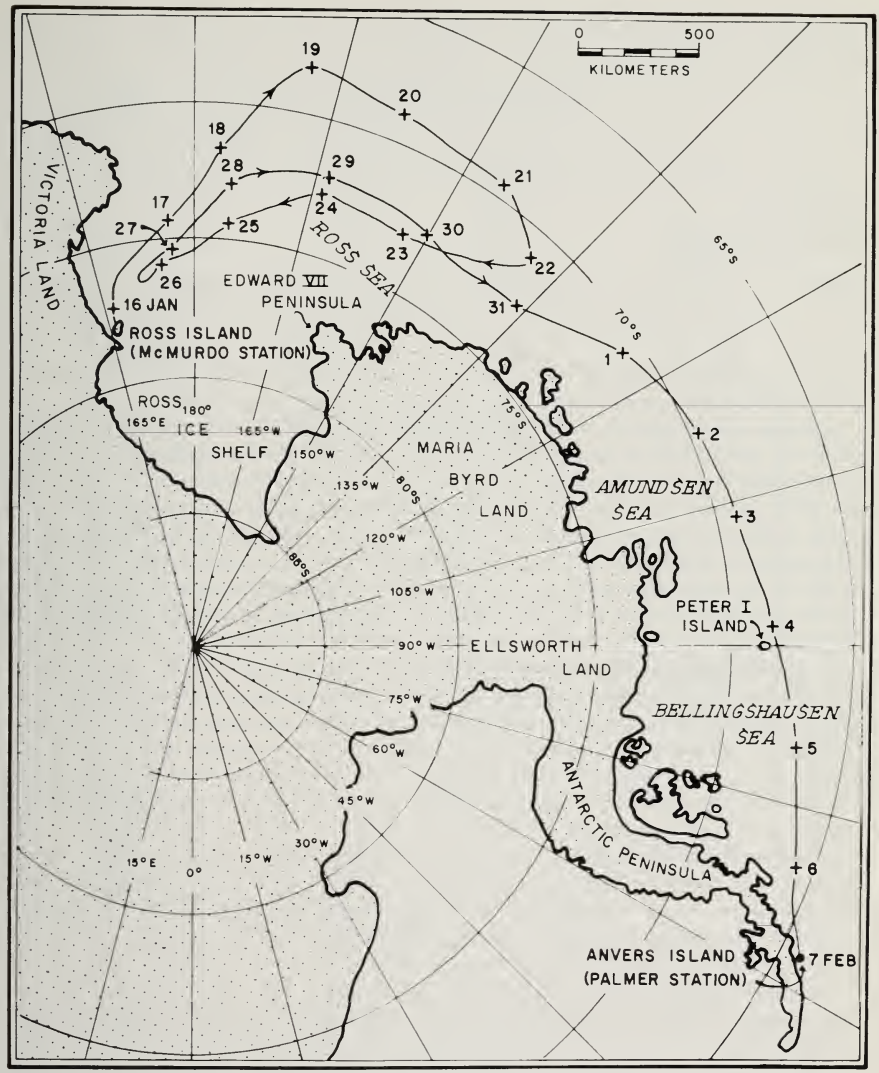


FIG. 1. Approximate route of the Glacier from McMurdo Station to Palmer Station. Numbers refer to dates between 16 January and 7 February 1976. Crosses (+) indicate noon (GMT) positions.

tions was somewhat arbitrary. Because of these factors, and insufficient data for each okta, data were grouped into 1–4, 5–8 oktas and open seas. Large leads (channels of water through ice floes) or polynyas (areas of open water in sea ice, distinguished from leads) were scored as open seas even though they existed within the pack ice, accounting for some of the apparent "open seas" occurrences of pack ice species, as it did in the study by Cline et al.

Table 1

Summary of Shipboard Observation Periods from McMurdo Station to Palmer Station (16 Jan.–6 Feb., 1976)

	Census h	Percent	Km^2 of census	Percent
Open water	14.7	10.8	243.5	12.1
Pack ice (1–4 oktas)	100.2	73.6	1438.5	71.2
Pack ice (5–8 oktas)	21.2	15.6	337.2	16.7
Total	136.1	100.0	2019.2	100.0

(1969). The Glacier followed routes of easiest passage through pack ice and habitats sampled were consequently biased towards open pack, leads and polynyas (Table 1).

Sightings of each species in the 3 habitats were totaled to ascertain general relationships (Table 2). Information on pelagic zonal distribution of each species in antarctic (continental and maritime) and subantarctic (transitional, cold and temperate) waters is given (after Watson 1975). General locations of known breeding sites along the census route are given in Table 2. Density estimates (given as mean ± SD) were computed for the 3 most common bird species by dividing the number of individuals seen during a census by the area censused (Table 3); for some other species only maximum densities are given, and for the remaining species densities were not computed because of low numbers or uncorrected biases in the probability of detection. For instance, although albatrosses were identifiable at 0.4 km, smaller birds, such as prions and storm-petrels, were not. The areas covered during the 69 censuses ranged from 8.6–94.5 km^2 ($\bar{x}$ = 29.3 ± 15.3 km^2). Observation periods were not uniformly spaced, either within or among days, hence there was insufficient basis for a daily comparison of species or abundances. To show general patterns in species pelagic ranges, the days for which each species was observed are given in Table 2. The Glacier often traveled 300+ km per day, thus only approximate range estimates are possible from this presentation: specific locations of important sightings are given in the text.

Data from Erickson et al. (1972) were used to calculate density estimates. They censused birds from 23 January–15 February 1972 in areas of pack ice, from its eastern edge in the Bellingshausen Sea at about 85°W to its western edge in the Amundsen Sea at 135°30′W. Their transects ranged from 68°S–72°S, which represented distances into the pack of from 39–330 km, respectively. Their 23 censuses sampled an area of 1255 km^2 over 88 h; the average census covered 54.6 ± 38.5 km^2 and lasted 3.8 ± 1.9 h. They did not partition their observations according to ice concentrations, hence throughout the present paper, references to their density and abundance figures are for pack ice in general (however, they stated that ice concentrations governed their penetration into the pack, hence their censuses were probably in pack ice of less than 60% concentration).

The densities given by Cline et al. (1969) in their study of birds of the summer pack ice in the Weddell Sea were converted from birds/$mile^2$ to birds/km^2. They related the occurrence of birds to pack ice concentrations as follows: light (10–30%), medium (40–60%) and heavy (70–100%). Parmelee (1977) provided observations of seabirds obtained during a study in the Weddell Sea, primarily in open water, between 23 January and 26 February 1973; there were no density estimates given or derivable from this study. Zink (1978) censused birds in the northwestern Weddell Sea during the austral summer of 1976 and presented data similar to those in the present report, however, pack ice densities represented averages

TABLE 2

NUMBER, DATES EACH SPECIES WAS SIGHTED AND OBSERVED HABITAT PREFERENCES[a]

Species	Number	Percent	Dates sighted Jan.–Feb. 1976	Percent within species: Open water (0 oktas)	Light pack (1–4 oktas)	Heavy pack (5–8 oktas)	χ^{2b}	Zonal distribution[c]: Ant-arctic	Sub-Antarctic	Known breeding sites[d]
Antarctic Petrel	3022	38.8	17–6	2.42	95.63	1.95	881.2*	C, M	N	KI, U
Adélie Penguin	2773	35.6	16–19, 22–31	—	54.00	46.00	1878.1*	C, M	N	AP, PI, RI, VL, 75°S/133°W
Snow Petrel	847	10.8	17–20, 22–4, 6	1.42	83.70	14.78	100.4*	C, M	Tr	AP, KI, VL
Arctic Tern	396	5.1	19, 20, 22, 23, 29–4	—	90.66	9.34	81.8*	C, M	Tr, C	N
Southern Fulmar	289	3.6	19, 3–6	22.49	77.51	—	75.6*	C, M	Tr, C, Te	AP, PI
Wilson's Storm-Petrel	116	1.5	22, 25, 27, 31, 3–6	62.07	37.93	—	277.7*	C, M	Tr, C, Te	AP, VL
South Polar Skua	110	1.4	16, 17, 29, 6	0.90	6.37	92.73	456.1*	C, M	Tr, C, Te	AP, KI, PI(?), RI, VL
Blue Petrel	77	1.0	22, 4	100.00	—	—	560.5*	C, M	Tr, C	N
Emperor Penguin	56	0.7	18, 22–1	—	60.71	39.29	24.6*	C	N	AP, KI, RI, VL
Southern Giant Fulmar	25	0.3	18, 19, 23, 27, 31, 2–5	12.00	72.00	16.00	NS	C, M	Tr, C, Te	AP
Black-browed Albatross	18	0.2	5, 6	100.00	—	—	129.2*	M	Tr, C, Te	N
Gray-headed Albatross	17	0.2	5, 6	100.00	—	—	120.6*	M	Tr, C	N
Cape Pigeon	15	0.2	22, 4–6	67.00	33.00	—	42.8*	C, M	Tr, C, Te	AP, PI
Unidentified mollymauk	12	0.2	4–6	100.00	—	—	—	—	—	N
Unidentified petrel	9	0.1	19, 20, 26	100.00	—	—	—	—	—	—
Light-mantled Sooty Albatross	2	0.1	5, 6	100.00	—	—	NC	C, M	Tr, C, Te	N
Wandering Albatross	1	0.1	5	100.00	—	—	NC	M	Tr, C, Te	N
Antarctic Prion	1	0.1	3	100.00	—	—	NC	C, M	Tr, C	N
Total	7786	100.0								

[a] Zonal distribution and known breeding sites are from Watson (1975) and Watson et al. (1971).

[b] Tests the hypothesis that birds were distributed randomly in the 3 habitat categories, based on area censused in each (see Table 1). Chi-square values are not calculated (NC) for species with "expected" values of less than 1 in one or more categories. Degrees of freedom are 2 in each case. An * denotes a $P < 0.005$.

[c] Key for zonal distribution—Antarctic: C = Continental, M = Maritime; Subantarctic: Tr = Transitional, C = Cold, Te = Temperate (from Watson 1975); N = Does not occur in subantarctic zone.

[d] Known breeding sites along route censused. Key: AP = Antarctic Peninsula, KI = King Edward VII Land, PI = Peter I Island, RI = Ross Island, VL = Victoria Land, U = uncertain, breeding possible, N = not known to breed along census route.

Table 3
Density Estimates for Selected Species[a]

Species	Density								
	Open water (N = 11)			Pack ice (1–4 oktas) (N = 46)			Pack ice (5–8 oktas) (N = 12)		
	$\bar{x}$	SD	(range)	$\bar{x}$	SD	(range)	$\bar{x}$	SD	(range)
Adélie Penguin	—	—	—	1.79[b]	± 3.38	(0–18.92)	4.05	± 4.46	(0–11.65)
Antarctic Petrel	0.31	± 0.24	(0–0.74)	1.57	± 4.99	(0–31.87)	0.23	± 0.53	(0–1.78)
Snow Petrel	0.10	± 0.25	(0–0.79)	0.48	± 0.45	(0–2.55)	0.38	± 0.41	(0–1.35)

[a] In birds/km².
[b] Based on N = 36; see range in Fig. 2.

over all oktas because of insufficient pack ice census data. Variance in densities, not given in the original report, have been calculated from the original census data.

There was continuous daylight from 16 January–1 February, but by 6 February there were 7 h of darkness per day. The daily mean sea water temperature from McMurdo to Palmer varied from −1.9–2.6°C (3–12 readings per day, N = 193; $\bar{x}$ = −0.95 ± 0.88°C). Because of the narrow range, bird distributions were not compared with sea water temperatures, as was done by Szijj (1967) in Pacific subantarctic waters. Data gathered during periods when visibility was less than 0.4 km were not included in the abundance or density estimates but were used for distributional records and behavioral information.

RESULTS

A total of 7786 individuals representing at least 16 species were sighted and their numbers and general habitat occurrence are given in Table 2. The hypothesis that each species was randomly distributed with respect to area censused, within each habitat category, was tested with Chi-square and rejected ($P < 0.005$) (see Table 2) in all species except the Southern Giant Fulmar (*Macronectes giganteus*). Thus, these arbitrarily chosen divisions do provide indications of general habitat preference.

The occurrence, absolute and relative abundance of each species are functions of census effort per habitat and geographic region studied, as well as of species spatio-temporal distributions and densities. Since most of the census effort was in pack ice (1775.7 of 2019.2 km²), it is not surprising that 4 species typical of pack ice (Antarctic Petrel [*Thalassoica antarctica*], Adélie Penguin, Snow Petrel [*Pagodroma nivea*], Arctic Tern) comprised 90.4% of the total birds observed; these species often occur in high densities. Many of the infrequently sighted species are characteristic of more open seas and/or lower latitudes. However, of all species observed, only the Black-browed (*Diomedea melanophris*), Gray-headed (*D. chrysostoma*) and Wandering (*D. exulans*) albatrosses typically are not found in continental antarctic waters (see zonal classification in Table 2). A con-

siderable range of latitudes (65°S–77°S) and longitudes (170°E–66°W) were censused, in addition to different habitats, hence the absolute ranking of species; perhaps the relative relationships reflect arbitrary distribution of sampling effort.

Species typical of pack ice.—Antarctic Petrel.—This was the most frequently sighted species during this cruise and occurred mostly in loose pack ice (Table 2). The 73 individuals sighted in open water were in groups of 4 or fewer. The mean density of 1.57 ± 4.99/km² in 1–4 oktas was biased by a concentration of 1750 birds sighted during a 3-h period on 27 January at 74°30′S, 179°0′W, in 2–4 oktas of pack ice (Table 3). Several large flocks of 300–400 birds roosting on large tabular icebergs and numerous other smaller flocks and individuals standing on pack ice were observed, accounting for the maximum density of 31.9/km². This concentration was unexplained. Without these flocks the mean density was 0.90 ± 2.04/km² and was typical of most pack ice (1–4 oktas) areas censused. The mean and maximum densities in 5–8 oktas, 0.23 ± 0.53/km² and 1.78/km², respectively, were less than those recorded for 1–4 oktas and were less variable. However, while the preference for light pack ice was clear (Table 2), the densities in light and heavy pack ice were not statistically different (t = 1.121, df = 58, NS).

Erickson et al. (1972) sighted this species on all but 2 of their 23 transects and recorded a mean density of 4.31 ± 6.55/km² and a maximum density of 23.06/km² in the pack ice of the Bellingshausen and Amundsen seas; the 4894 individuals they counted constituted 47.7% of the total birds they observed. Of the 23 density estimates calculated from their data, only 5 exceeded 4.0/km² (5.76, 12.49, 15.48, 18.56 and 23.06).

Cline et al. (1969) observed no large concentrations of Antarctic Petrels in the Weddell Sea and recorded a mean density of 0.35/km² (no variance given); they noted this species most often in light pack ice. In the pack ice of the northwestern Weddell Sea, Zink (1978) observed this species most frequently in 1–4 oktas and recorded a mean density of 3.0 ± 11.03/km² and a maximum density of 58/km². Parmelee (1977) also found them common in the Weddell Sea. Present data are insufficient to determine if there are significant differences between densities of Antarctic Petrels in the Weddell Sea and the Ross, Bellingshausen and Amundsen seas, although there is a preference by this species for light pack ice concentrations.

Adélie Penguin.—Occurrence of Adélie Penguins during this cruise is shown in Fig. 2. Erickson et al. (1972) reported this species as rare in the pack ice of the Bellingshausen and Amundsen seas; they observed 24 individuals in 1255 km² of pack ice census. A possible reason for this is the apparent lack of breeding sites along the coasts of the Bellingshausen

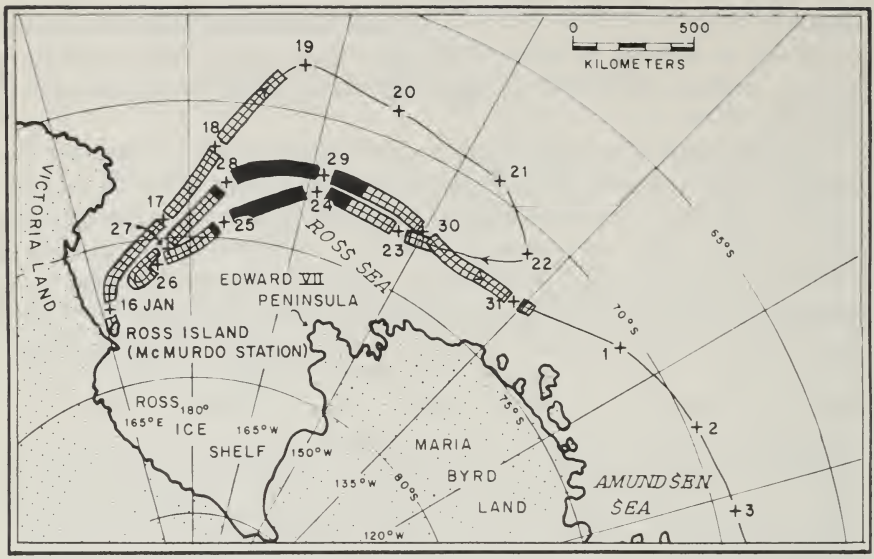


FIG. 2. Occurrence of Adélie Penguins along the cruise track is shown by ⊟⊟. ■ indicates a region where Adélie densities were significantly higher than other areas in which they were sighted.

and Amundsen seas (G. E. Watson, pers. comm.). The absence of Adélies from these areas was substantiated during the present study, as most of the Adélies (2746 of 2773) were observed in the Ross Sea. Twenty-seven Adélies were sighted between 135°W and 127°W in 7.3 h (118.1 km²) and none was seen east of 127°W during 18.3 h (294.2 km²) of pack ice census. This species reportedly breeds on Peter I Island (Watson 1975), however, none was observed from the Glacier (see Fig. 1) or during a helicopter seal census covering 65 km² at approximately 67°47′S, 90°47′W, which is roughly 100 km north of Peter I. Because of the apparent absence of Adélies from the Bellingshausen and Amundsen seas, censuses in these areas were not used to calculate density estimates. In the Ross Sea, density estimates ranged from 0–18.9/km² and the mean densities were 1.79 ± 3.38/km² in 1–4 oktas and 4.05 ± 4.46/km² in 5–8 oktas of pack ice (Table 3); the difference between these mean densities was insignificant (t = 1.85, df = 48, NS). On several occasions Adélies were observed in 3–5 oktas during 1 census, and it was difficult to assign these observations to either (1–4 or 5–8) pack ice category. Thus, while there appeared to be more Adélies in heavy pack ice (Table 2), the insignificant relationship may reflect consolidation of observations into 1–4 and 5–8 oktas, whereas, possibly Adélies prefer concentrations of 3–5 oktas. Further-

more, the distribution of Adélies in the Ross Sea was not uniform. The blackened portion of Fig. 2 represents an area where Adélies appeared to be concentrated. Within these areas a density of 5.60 ± 5.13/km² was recorded (N = 15), whereas the density was 1.24 ± 1.78/km² for the remainder (N = 25) of the Ross Sea; using a *t*-test for unequal variances and sample sizes (Snedecor and Cochran 1967:114–116) these differences were statistically significant ($t = 3.179$, df = 40, $0.005 < P < 0.01$). This concentration possibly consisted of nonbreeders attracted to a localized food source.

Cline et al. (1969) found Adélies to be the most abundant bird in the summer pack ice of the Weddell Sea and recorded a mean density of 10.96/km² (no variance given) and a maximum of 90.81/km²; they found them most frequently in heavy pack ice. They noted that the distribution of Adélies was uneven and that the greatest numbers were seen in the northern limits of the pack. Their maximum density estimate consisted of 1360 individuals observed on 15 March 1968, roughly 350 km from nearby breeding sites on the Antarctic Peninsula. They noted that this concentration could have comprised dispersing adults from peninsular breeding colonies. Zink (1978) observed large numbers of Adélies in loose pack ice, at the northern limits of the pack ice in the Weddell Sea, and estimated mean and maximum densities of 7.0/km² and 101.75/km², respectively. (The mean density was corrected downwards to reduce the effect of several large concentrations; original figure was mean density of 28 ± 30.6/km² [Zink, unpubl.].) The apparent occurrence of higher densities in the Weddell Sea, as compared to the Ross, Bellingshausen and Amundsen seas, needs further documentation, as both Cline et al. (1969) and Zink (1978) censused near breeding localities and high densities recorded in these areas could have inflated mean densities.

Adélies usually were seen in groups of 6–20 birds, often on the leeward side of ice hummocks and pressure ridges. Like the Antarctic Petrel, Adélies seemed to prefer older pack ice, especially ice with uneven surfaces providing shelter. Few Adélies were observed in the water except when forced to dive as the Glacier approached to within 100 m. Cline et al. (1969) also observed this behavior in the Weddell Sea and noted that Adélies during their post-breeding molt typically remain out of the water and fast. I observed little direct evidence of molting. That few Adélies were seen in the water could be a result of either restricted feeding periods or the difficulty in seeing swimming penguins. On several occasions, Adélies were seen to approach the ship when it was stuck in ice, hence, curiosity and/or lack of fear may explain their reluctance to flee an approaching ship.

Leopard seals (*Hydrurga leptonyx*) prey on adult Adélies at sea, how-

ever, the incidence of this, and adult mortality in general, are thought to be low (Watson 1975). On 25 January, 2 crew members on the bridge of the Glacier observed a killer whale (*Orcinus orca*) lunge out of the water and apparently capture 2 Adélies standing at the edge of a floe. Further observations are needed to document the validity of this claim and extent of this predation.

Snow Petrel.—This species is a common antarctic bird generally restricted to cold continental and maritime waters with pack ice and/or icebergs present (Watson 1975). It was sighted on all but 2 days. Most Snow Petrels (98.58%) were seen over pack ice and their distribution was usually uniform. The densities in pack ice were 0.48 ± 0.45/km² in 1–4 oktas and 0.38 ± 0.41/km² in 5–8 oktas (Table 3); there was no significant difference between these densities ($t = 0.697$, df = 56, NS). Of the 847 Snow Petrels recorded, the largest flock had 40 individuals and only 5 other flocks had 10 birds or more (10, 12, 13, 19 and 25). In the pack ice of the Bellingshausen and Amundsen seas, Erickson et al. (1972) recorded 3516 Snow Petrels, which represented 34.2% of the total number of birds they observed. Their mean density was 2.83 ± 3.53/km² and the maximum was 15.92/km², suggesting that this species is more abundant in the Bellingshausen and Amundsen seas. The pelagic distribution map given in Watson (1975) appears to exclude the southern Ross Sea. In the Weddell Sea, Cline et al. (1969) recorded a mean density of 2.82/km² and a maximum density of 46.68/km² and noted this species most frequently in light and medium pack ice concentrations. The Snow Petrel was the most common (24.5% of total) volant species sighted by Zink (1978); a mean density of 8.0 ± 5.50/km² and a maximum density of 98.69/km² (not included in the mean density estimate) were recorded in pack ice, primarily in ice concentrations of from 1–5 oktas. Few birds were sighted in open waters and a maximum density of 5.93/km² was recorded. The largest group of Snow Petrels observed by Parmelee (1977) in the Weddell Sea was 47 and a total of 1588 birds was sighted (sightings made on 32 of 35 days).

The specific habitat preference of Snow Petrels during this study was not clear as the observed frequencies in pack ice (83.7:14.9) paralleled the relative areas censused in each habitat (71.2:16.7). Although this difference was significant ($\chi^2 = 100.23$, df = 1, $P < 0.005$) the preferred habitat may have been masked by consolidating the pack ice observations into 2 categories. As with the Adélie Penguin, perhaps 3–5 oktas is a better approximation of their habitat (ice concentration) preference.

Snow Petrels use 2 types of flight. One was "very erratic, almost batlike" (Watson 1975); the birds flew low over the surface, often exhibiting high maneuverability as they closely followed ice edges. This apparent foraging behavior is consistent with the observation of Falla (1964) that

their primary food consists of dead or injured macroplankton. As Ainley et al. (1978) noted, such plankton would be expected to accumulate at the edges of cakes of ice. The other type of flight, steady and direct, was used about 7–10 m above open water and occasionally over pack ice.

Snow Petrels frequently hunted along narrow strips of pack ice while avoiding adjacent open water. Upon sighting a prey item a flying individual quickly veered upwards and then fluttered down to the surface. Feeding motions included pecking at the surface and submerging the head and neck to catch subsurface prey, which, according to Watson (1975), consists mainly of fish and some invertebrates. Birds that remained on the surface for 15 sec or longer folded their wings and swam about after prey. Foraging individuals that alighted on the surface for less than 15 sec usually kept their wings unfolded and held at about 60° to the surface. This was also noted by Ainley et al. (1978) and apparently facilitates more rapid or efficient take-offs.

Arctic Tern.—Adult Arctic Terns migrate annually from their arctic breeding grounds to "winter" in the Antarctic during the austral summer. The Arctic Tern was the fourth most abundant species observed and was seen mostly in loose pack ice (Table 2) along the northern edge of the pack; few were encountered south of the pack edge. The maximum density recorded was 2.72/km² on 3 February. Ainley et al. (1978) noted that there are no records of Arctic Terns from the Ross Sea. The westernmost observations of terns were on 22–23 January, when 56 birds were sighted between 72°S–72°50′S and 144°40′W–151°6′W. These observations perhaps establish the limit of Arctic Tern distribution in the eastern Ross Sea. Darby (1970) observed only 1 Arctic Tern in 4 north-south traverses of the Ross Sea and that sighting was (actually in the southern Pacific) at 67°55′S, 174°41′E on 18 January 1968.

Arctic Terns occurred in flocks of 5–20 birds; 5 flocks of more than 20 were seen (60+, 52, 41, 30 and 25); a total of 60 birds was observed in groups of fewer than 5. The flock of 60+ terns was on an iceberg near Peter I Island during a helicopter seal census and was not included in the shipboard census data. Erickson et al. (1972) recorded a mean density of 1.27 ± 1.91/km² and a maximum density of 7.95/km².

Cline et al. (1969) recorded a mean density of 0.97/km² and a maximum density of 13.90/km², mostly in light and medium pack ice concentrations. Zink (1978) observed a mean density of 1.4 ± 1.14/km² and a maximum of 3.39/km² in pack ice, as well as a mean density of 2.67 ± 5.36/km² and a maximum density of 27.54/km² in open seas. These observations support the conclusion that Arctic Terns are most abundant in the Weddell Sea (Watson 1975, Parmelee 1977).

Arctic Terns often passed the Glacier at the outer limits of the transect

strip and it was not always possible to see plumage characteristics clearly. Individuals observed closely were in non-breeding plumage and most appeared to be in heavy wing and tail molt. The few feeding individuals observed plunged headfirst into the water from a height of about 3.5 m. Some birds worked low over brash ice and hovered above prey items before picking them off the surface in flight.

Southern Fulmar (*Fulmarus glacialoides*).—Most (287 of 289) of the sightings of Southern Fulmars occurred between 3–6 February. The 2 birds seen west of 91°W were in loose pack ice on 19 January at 68°30′S, 161°30′W and 68°45′S, 159°0′W. Watson (1975) states that this species is highly pelagic and avoids pack ice, but Johnstone and Kerry (1974) remark that Southern Fulmars occur commonly in pack ice in the Australian sector of the southern ocean. The majority of the fulmars sighted east of 91°W (222 of 287), during the present study, were in loose pack ice (1–2 oktas), and of these, 151 were in groups of fewer than 5 and the remainder were in 9 flocks of fewer than 40. Most birds were sitting on the water or on pack ice and few feeding birds were observed. Some fulmars followed the ship briefly.

Erickson et al. (1972) observed this species on 9 of 23 transects, and of the total of 53 individuals sighted, the maximum density was 0.42/km² (25 birds sighted in 60 km²). The scarcity of sightings west of 91°W might be explained by the relative lack of censuses in more northerly ice-free waters (west of 91°W). In the Weddell Sea, Zink (1978) observed 3 of 709 birds in pack ice and Cline et al. (1969) sighted none in pack ice.

South Polar Skua (*Catharacta maccormicki*).—Watson (1975) states that during the austral summer breeding season, adult South Polar Skuas remain near breeding colonies, while sub-adults are found at sea. Of the 110 skuas observed, 102 were within 75 km of McMurdo Station, either in dense pack ice or along the fast ice in McMurdo Sound. Skuas observed near McMurdo Station were light phase birds. Of the remaining 8 skuas sighted, 6 were seen within 115 km of McMurdo, 1 in the western Ross Sea and 1 in the western Bellingshausen Sea. The skua in the western Ross Sea (at 72°10′S, 157°20′W) was in loose pack ice (1 okta), and was a dark phase bird that showed prominent golden hackles and appeared to be in fresh plumage. Presumably an adult (based on plumage, see Watson 1975), it was some 560 km from the nearest known breeding site.

Skuas are more often found near land, thus, there are relatively few pelagic sightings. Erickson et al. (1972) observed 8 individuals. In the Weddell Sea, Cline et al. (1969) observed 4 and Zink (1978) sighted 10. In spite of the paucity of pelagic sightings, individuals banded in Antarctica have been recovered from temperate seas (Watson 1975) and Greenland (Parmelee et al. 1977).

Emperor Penguin (*Aptenodytes forsteri*).—The largest number of Emperor Penguins seen at 1 time was 4. Most sightings were of groups of 2 or 3, widely dispersed in the pack ice of the Ross and Amundsen seas. Most individuals occurred in light pack ice. Erickson et al. (1972) recorded 30 Emperor Penguins in the Bellingshausen and Amundsen seas. There are no known breeding sites along the coasts of these seas and this species apparently does not range far from its breedings sites, except for wandering young birds. Larger concentrations were noted in the Weddell Sea by Parmelee (1977, maximum number sighted at 1 time was 67, total sightings were 363). Also in the Weddell Sea, Cline et al. (1969) found Emperor Penguins most often in light and moderate pack ice concentrations and recorded a mean density of 0.5/km^2 and a maximum of 5.33/km^2. Zink (1978) observed a mean density of 0.14 ± 0.17/km^2 and a maximum of 0.50/km^2.

Southern Giant Fulmer.—Watson (1975) stated that this species is highly pelagic throughout antarctic and subantarctic waters and that young individuals usually are distributed farther north than adults. Fourteen of 17 (82.3%) Giant Fulmars sighted in the Ross Sea were juveniles, based on entirely (or nearly so) dark plumage (Watson 1975). There are both dark and white phases of the Southern Giant Fulmar and the young of each phase resemble the adult condition. The birds sighted during the present study were all dark phase. Siple and Lindsey (1937) and Watson (1975) suggested that the percentage of white phase birds increases to the south or in pack ice; the present observations do not substantiate this. Four of the other 8 Giant Fulmars observed in the Amundsen and Bellingshausen seas were adults. Giant Fulmars appeared to be distributed randomly within the 3 habitat types, although this is inconclusive because of the small sample size (25).

Erickson et al. (1972) observed 65 individuals in 1255 km^2 of pack ice census in the Bellingshausen and Amundsen seas. In the summer pack ice of the Weddell Sea, Cline et al. (1969) sighted 8 individuals. Zink (1978) observed 106 Southern Giant Fulmars in the Weddell Sea and found them randomly distributed between open seas and light and heavy pack ice.

Species typical of open seas.—Wilson's Storm-Petrel (*Oceanites oceanicus*).—Wilson's Storm-Petrels were observed in open water or loose pack ice (Table 2); their occurrence closely followed the pelagic distribution given by Watson (1975). Twenty-nine birds were sighted between 178°27′E and 176°25′W (73°10′S–75°S) and 1 bird was seen between 176°25′W and 97°59′W (at 72°0′S, 145°0′W, on 22 January in 1 okta of pack ice) and the remainder (86) were seen between 97°59′W and Palmer Station. The southernmost sighting was at 76°23′S, 171°53′E, about 150 km from McMurdo Station on 26 January. This is near the southwestern limit of the pelagic

range, and is approximately 450 km from a breeding site on the coast line of Victoria Land, at 72°S, 170°E (Watson 1975). Ainley et al. (1978) noted Wilson's Storm-Petrels at Cape Crozier (Ross Island) and therefore the limits of its pelagic range in the Ross Sea are equivocal.

Erickson et al. (1972) observed 7 individuals in the pack ice of the Bellingshausen and Amundsen seas. Cline et al. (1969) observed few birds in the pack ice of the Weddell Sea. Zink (1978) recorded a mean density of 0.44 ± 1.15/km² and a maximum density of 4.38/km² in the pack ice of the Weddell Sea in addition to a mean density of 1.44 ± 1.97/km² and a maximum density of 9.65/km² in open seas. These studies indicate that the occurrence of Wilson's Storm-Petrels in pack ice is limited. Once, (about 65°30′S, 67°20′W) approximately 50 birds were in view, mostly astern and following the ship. Otherwise the maximum in view was about 4.

Blue Petrel (*Halobaena caerulea*).—All Blue Petrels seen in this study and in the Weddell Sea by Zink (1978) were in open seas. A flock of 55 Blue Petrels was sighted at 70°40′S, 136°52′W on 22 January as the Glacier passed through an extensive patch of open water in the eastern Ross Sea. This sighting is approximately 300 km south of the previous southernmost record (see Watson et al. 1971, Watson 1975). The other 22 individuals were sighted on 4 February, in several small flocks, in the Bellingshausen Sea.

Unidentified petrels.—Unidentified petrels were seen on 9 occasions in the southern Ross Sea on 19, 20 and 26 January. Poor viewing conditions precluded positive species determination but probably only the Mottled Petrel (*Pterodroma inexpectata*) and/or Sooty Shearwater (*Puffinus griseus*) were involved. All of these sightings are south of the known range of the Sooty Shearwater by at least 400 km. Noteworthy is the sighting on 26 January at 76°10′S, 173°30′E, as this location is about 100 km south of the pelagic range of the Mottled Petrel, but is 1500 km south of the known pelagic range of the Sooty Shearwater. During 4 cruises from New Zealand to McMurdo, between January and March 1968, Darby (1970) recorded her southernmost Sooty Shearwater at 68°22′S, 170°18′E, however, she observed no Mottled Petrels.

Antarctic Prion (*Pachyptila desolata*).—A single Antarctic Prion was seen on 3 February at 68°50′S, 100°20′W over open water. Erickson et al. (1972) did not see this species. In the large leads and polynyas of the Weddell Sea pack ice, Cline et al. (1969) recorded 24 prions and a mean density of 0.04/km². Zink (1978) recorded a mean density of 0.21 ± 0.40/km² during open water transects in the Weddell Sea and Parmelee (1977) observed 304 prions, which included a single observation of 100+ birds.

Cape Pigeon (*Daption capense*).—On 22 January, at 70°40′S, 136°52′W, a Cape Pigeon was seen over open seas. This sighting represents a south-

ern extension of approximately 200 km based on the map in Watson (1975). However, Ainley et al. (1978) noted records of Cape Pigeons in the Ross Sea at 72°S and 76°54′S. Other records include sightings by Darby (1970) at 73°46′S and by the first Byrd Antarctic Expedition (*in* Siple and Lindsey 1937) in Discovery Inlet, at 78°30′S. From these records it is possible to conclude that only a few Cape Pigeons, perhaps sexually immature individuals, wander through the southern Ross Sea. As noted by Ainley et al. (1978) the observation of Spellerberg (1971) that Cape Pigeons were abundant off the northern tip of Ross Island during March 1964, is suspect. Of the other 14 Cape Pigeons sighted during the present study, 5 were in light pack ice and 9 were over open waters in the Bellingshausen Sea. Erickson et al. (1972) sighted a Cape Pigeon in the pack ice of the Amundsen Sea at 67°47′S, 128°50′W on 11 February 1972. In the northwestern Weddell Sea, Zink (1978) sighted 694 Cape Pigeons in open seas and recorded a mean density of 1.0 ± 1.22/km² and a maximum density of 4.2/km²; few were observed in pack ice. Cline et al. (1969) observed a total of 25 Cape Pigeons and a mean and maximum density of 0.04/km² and 1.70/km², respectively.

Albatrosses.—Four species of albatrosses (Black-browed, Gray-headed, Wandering and Light-mantled Sooty [*Phoebetria palpebrata*]) were sighted during open water censuses in the Bellingshausen Sea from 4–6 February. These species are typically highly pelagic and avoid pack ice (Watson 1975). The largest number of adults of either the Black-browed Albatross or Gray-headed Albatross in view at 1 time was 3. The actual number of albatrosses observed is difficult to determine, because of their well known ship-following habits (except for the gray-headed). Also, 2 or 3 Black-browed or Gray-headed albatrosses were observed (discontinuously) within a short time and there was suspicion as to whether there were 1, 2 or 3 individuals involved. Immature Black-browed and Gray-headed albatrosses are difficult to distinguish at sea, and the records of "unidentified mollymauk" in Table 2 refer to juveniles of these species.

DISCUSSION

Pelagic seabird observations obtained during the austral summer in Antarctica are difficult to interpret because the relative abundances of immatures, unsuccessful breeders and foraging breeders are unclear. Darby (1970) suggested that many birds seen far from land during the breeding season were probably non-breeding or immature individuals. Delayed sexual maturity is typical for most seabirds. Consequently, it is probable that sexually immature procellariids and penguins constitute a high proportion of birds seen at sea, since they evidently avoid regions near breeding sites

(Watson 1975). Because of the short austral breeding season, it is likely that most unsuccessful breeders depart to sea rather than renest. Brook and Beck (1972) discovered nesting Antarctic Petrels, Snow Petrels and South Polar Skuas in the Theron Mountains, 250 km from the nearest foraging grounds in the open waters of the Weddell Sea. Warham et al. (1977) speculated that breeding Mottled Petrels, from colonies on islands south of New Zealand, may range up to 2200 km into the southwestern Ross Sea during off-duty periods. Beck (1969) noted that Cape Pigeons in breeding condition have been collected 350 km from the nearest breeding site. Breeding petrels range considerable distances from nest-sites and undoubtedly contribute to the number of birds seen at sea; this contribution may increase as observations are made nearer to breeding sites. It is not generally possible to distinguish ages or sexes of most species on the basis of sight observations. Therefore, the relative abundance of adults and immatures is uncertain. Sightings of birds hundreds of km from the nearest land (not necessarily breeding sites; see Table 2 for breeding sites of species sighted during this study) provide data for species-level regional distributions and information about species' pelagic ecology and behavior. These data can also be used to ascertain regional patterns in the composition of pelagic seabird communities.

Density estimates are useful for providing a quantitative measure of avian occurrence. Densities (birds/area) are superior in most instances to measures of birds per unit of time or linear distance because of potentially serious biases in observer proficiency and ability, ship speed and uncorrected biases in the nonuniform probability of sighting different species at a given distance. Densities can also be extrapolated to estimate the number of birds in a given region. Erickson et al. (1972) stated that the area circumscribed by the outer limits of their sampling effort was about 250,000 km^2. If the mean density for the Antarctic Petrel (4.31/km^2) is applied to this area, the resulting number of birds is 1,077,500. However, it should be recognized that there is considerable variance (SD = 6.55) about this mean. The Antarctic Petrel often occurs in dense aggregates and additional censuses are probably required. It is necessary to establish the uniformity of the habitat within the bounds of the census effort and to account for such clumped distributions of birds (or at least acknowledge them). Also, because the age structure of this pelagic "population" is unknown, such population estimates are probably area specific and not necessarily applicable to other geographic regions.

In antarctic ecosystems, there are typically few species, but these are often abundant (Watson 1975, Cline et al. 1969). In the present study, most of the census effort (88% of the total census area) was in pack ice. Ten species were observed in pack ice and of these, 4 (Antarctic Petrel,

Adélie Penguin, Snow Petrel and Arctic Tern) accounted for over 90% of birds observed in pack ice. Erickson et al. (1972) found the same 10 species in the pack ice of the Bellingshausen and Amundsen seas, although few Adélie Penguins. In order of decreasing abundance, the Antarctic Petrel, Snow Petrel and Arctic Tern accounted for 98.2% of the 10,270 total birds they observed. In the pack ice of the Weddell Sea, the Adélie Penguin, Snow Petrel and Antarctic Petrel accounted for 69.4% of the 14,376 total birds (pack ice and open seas) observed by Zink (1978) even though only 21.6% of the 698 km^2 of census area was in pack ice. Also in the summer pack ice of the Weddell Sea, Cline et al. (1969) found that the Adélie Penguin, Snow Petrel, Arctic Tern, Emperor Penguin and Antarctic Petrel accounted for 98.8% of the 9451 total birds sighted. These studies substantiate the claim that the pack ice environment is dominated by a few, rather abundant species. However, the same species are not equally dominant between areas nor are the relative abundances equal.

Cline et al. (1969) concluded that pack ice concentrations influenced bird distributions and densities and they found the highest densities of most species in ice concentrations of 10–60%. The observations of Ainley et al. (1978) further support this conclusion. During the present study, ice concentrations of 1–5 oktas supported the greatest numbers of birds. However, the type of pack ice also was important. Pack ice varies considerably in thickness, surface and subsurface structure; these vary with age of ice and amount of compacted snow. Different kinds of ice probably offer different potentials to birds, in terms of resources or shelter. Older pack ice (2 years and up) is thicker and generally has a rough, irregular surface that provides wind shelters for resting or molting birds. In addition, its subsurface has usually deteriorated into a matrix of small holes and channels which are often frequented by various invertebrates (Watson 1975) such as krill (pers. obs.). There were qualitative indications that more birds were in areas of older pack ice than in newer (thinner and flatter) pack ice. Future studies should determine the type of ice as well as its concentration for correlations with the occurrence of birds, seals and whales.

Voous (1965) suggested that food availability and abundance are probably the primary factors influencing the distribution of birds in antarctic waters. From the above discussion, it is apparent that the pelagic occurrence of seabirds results from an interaction of food availability and ice concentration and structure.

There was insufficient census effort in open waters to determine, with much certainty, the species characteristic of this environment. Species typical of open, continental antarctic waters are the Southern Fulmar, Wilson's Storm-Petrel, Blue Petrel, Southern Giant Fulmar, Cape Pigeon,

Antarctic Prion and Light-mantled Sooty Albatross (Watson 1975). In general, seabird diversity is greater in antarctic maritime and subantarctic waters than in antarctic continental waters (Darby 1970, Szijj 1967, Watson 1975). Darby (1970) thought that the northern limit of the pack ice constituted a barrier to the southward expansion of many species and noted that several species were consistently 80–100 km north of the pack, whatever its northern limit. On 4 February, the Glacier passed out of what was probably the northern extent of pack ice (68°S, 87°W). The species composition changed rapidly (within 2 km) from predominantly pack ice species to species characteristic of open seas. The interface between pack edge and open water potentially supports large numbers of birds because of an accumulation of plankton (Routh 1949). However, no such concentrations of birds were noted.

The interactions and associations of various species at sea are poorly understood. In the Bellingshausen and Weddell seas (Zink, unpubl.) Wilson's Storm-Petrel appeared to be an "indicator" of localized patches of food. Individuals seemed to search independently and were randomly interspersed until a patch of food was located. Others then flocked to the site and fed as described by Alexander (1954) and Murphy (1936). They headed into the wind, pattering their feet on the surface and feeding through the patch of food and then returned downwind and worked through this specific area again. Such a grouping of Wilson's Storm-Petrels often attracted other species such as the Cape Pigeon and Southern Giant Fulmar, and albatrosses in more northerly areas. Both the nature of specific roles in such assemblages and the geographic trends in composition of interspecific flocks are unknown.

SUMMARY

Observations of 16 species of seabirds in antarctic waters were obtained during the austral summer of 1976 while the USCGC Glacier cruised from McMurdo Station (Ross Island) to Palmer Station (Anvers Island). Information on distribution, abundance, habitat (ice concentration) preference and behavior of these species is given and comparisons are made with recent seabird surveys in the Bellingshausen, Amundsen and Ross seas and the Weddell Sea.

The Antarctic Petrel, Adélie Penguin and Snow Petrel were the most abundant species, respectively, in pack ice, where most of the 136.1 h of observation occurred. The Adélie Penguin, which was generally absent from the Amundsen and Bellingshausen seas, and the Antarctic Petrel both occurred in large concentrations, while the Snow Petrel was more uniformly spread throughout the pack ice encountered on this cruise. These species, the Arctic Tern and the Emperor Penguin, probably are the primary species of the antarctic pack ice ecosystem. Antarctic avifaunas are dominated by relatively few species. However, the same species were not dominant throughout all regions examined and in many cases the relative dominances were different. A part of these regional differences may be attributed to the distribution of sampling effort between different regions and habitats. Pack ice con-

centrations of 1–5 oktas appeared to support the greatest numbers of birds. There were indications that older, thicker ice is preferred by birds because its irregular surface provides shelter and its subsurface structure is inhabited by various invertebrate prey items of seabirds.

Because there were few censuses in open seas, only general indications of characteristic species were obtained. The Wilson's Storm-Petrel, Blue Petrel, Black-browed Albatross, Gray-headed Albatross, Cape Pigeon, Light-mantled Sooty Albatross, Wandering Albatross and Antarctic Prion were sighted either entirely or mostly over open waters.

The relative abundance of adults and immatures in pelagic observations is unknown because they are not distinguishable at sea. Also, both sexually immature birds and foraging breeders can be expected to occur long distances from breeding sites.

ACKNOWLEDGMENTS

This study was financed by NSF grant No. OPP74-21374, through the United States Antarctic Research Program (USARP) to D. F. Parmelee. I thank Dr. Parmelee for his advice and assistance throughout the project and Dr. G. Llano for his efforts in planning the field season. The entire crew of the USCGC Glacier was very helpful, although I would like especially to thank Captain C. P. Gillett, Cdr. J. Coste and Lt. B. Genez for their assistance. S. M. Kozlechar assisted with observations on occasion and his help is greatly appreciated. Drs. T. Foster and J. Middleton, and Lt. R. Buhl offered helpful advice throughout the cruise. I thank D. G. Ainley, G. F. Barrowclough, L. M. Conroy, D. F. Parmelee, R. M. Timm and H. B. Tordoff for comments on earlier drafts of the manuscript. I am especially grateful to G. E. Watson for providing a detailed and critical review of this paper. Valuable discussions were held with S. L. Frye, P. H. Jacobsma, H. Kermott, N. E. Lederer, R. J. Oehlenschlager, D. B. Siniff, R. M. Timm, D. W. Warner and M. D. Witt regarding various aspects of this study. K. A. Kohn prepared Fig. 1 and the map on which Fig. 2 is based. A. Fosdick typed several drafts.

LITERATURE CITED

Ainley, D. G., R. C. Wood and W. J. L. Sladen. 1978. Bird life at Cape Crozier, Ross Island. Wilson Bull. 90:492–510.

Alexander, W. B. 1954. Birds of the ocean. 2nd rev. ed. Putman, New York, New York.

Beck, J. R. 1969. Food, moult and age of first breeding in the Cape Pigeon, *Daption capensis* Linnaeus. Br. Ant. Surv. Bull. 21:33–44.

Bierman, W. H. and K. H. Voous. 1950. Birds observed and collected during the whaling expeditions of the 'Willem Barendsz' in the Antarctic, 1946–1947 and 1947–1948. Ardea 37:1–123.

Brook, D. and J. R. Beck. 1972. Antarctic Petrels, Snow Petrels, and South Polar Skuas breeding in the Theron Mountains. Br. Ant. Surv. Bull. 27:131–137.

Cline, D. R., D. B. Siniff and A. W. Erickson. 1969. Summer birds of the pack ice in the Weddell Sea, Antarctica. Auk 86:701–716.

Darby, M. M. 1970. Summer seabirds between New Zealand and McMurdo Sound. Notornis 17:28–55.

Erickson, A. W., J. R. Gilbert, G. A. Petrides, R. J. Oehlenschlager, A. S. Sinha and J. Otis. 1972. Populations of seals, whales and birds in the Bellingshausen and Amundsen seas. Ant. J. of the U.S. 7:70–72.

Falla, R. A. 1964. Distribution patterns of birds in the antarctic and high latitude subantarctic. Pp. 367–378 *in* Biologie Antarctique (R. Carrick et al., eds.). Hermann, Paris, France.

Gain, L. 1914. Oiseaux antarctiques. Deuxieme Exped. Ant. Fr. 1908–1910, 2:1–100.

Holgerson, H. 1945. Antarctic and sub-antarctic birds. Sci. Result. Norw. Ant. Exped. 1927–28, 2(23):1–100.

———. 1957. Ornithology of the 'Brategg' Expedition. Sci. Result. 'Brategg' Exped. 1947–48, 4:1–80.

Johnstone, G. W. and K. R. Kerry. 1974. Ornithological observations in the Australian sector of the southern ocean. Proc. 16th Int. Ornithol. Congr., Canberra, Australia.

Murphy, R. C. 1936. Oceanic birds of South America. Vol. 1, Am. Mus. Nat. Hist., New York, New York.

Parmelee, D. F. 1977. Adaptations of Arctic Terns and Antarctic Terns within Antarctic ecosystems. Pp. 687–702 *in* Adaptations within Antarctic ecosystems. Gulf Publ. Co., Houston, Texas.

———, W. R. Fraser and D. R. Neilson. 1977. Birds of the Palmer Station area. Ant. J. of the U.S. 12:14–21.

Routh, M. 1949. Ornithological observations in the antarctic seas. Ibis 91:577–606.

Siple, P. A. and A. Lindsey. 1937. Ornithology of the second Byrd Antarctic expedition. Auk 54:147–159.

Snedecor, G. W. and W. G. Cochran. 1967. Statistical methods. The Iowa State Univ. Press, Ames, Iowa.

Spellerberg, I. F. 1971. Arrival and departure of birds at McMurdo Sound, Antarctica. Emu 71:161–171.

Szijj, L. J. 1967. Notes on the winter distribution of birds in the western Antarctic and adjacent Pacific waters. Auk 84:366–378.

Voous, K. H. 1965. Antarctic birds. Pp. 649–689 *in* Biogeography and ecology in Antarctica (P. van Oye and J. van Mieghem, eds.). Dr. Junk, The Hague, Holland.

Warham, J., B. R. Keeley and G. J. Wilson. 1977. Breeding of the Mottled Petrel. Auk 94:1–17.

Watson, G. E. 1975. Birds of the Antarctic and Sub-antarctic. Am. Geophys. Union, Washington, D.C.

———, J. P. Angle, P. C. Harper, M. A. Bridge, R. P. Schlatter, W. L. N. Tickell, J. C. Boyd and M. M. Boyd. 1971. Ant. Map Folio Series 14:1–18.

Zink, R. M. 1978. Birds of the Weddell Sea. Ant. J. of the U.S. 13:142–145.

J. F. BELL MUSEUM OF NATURAL HISTORY, UNIV. MINNESOTA, MINNEAPOLIS, MINNESOTA 55455. (PRESENT ADDRESS: MUSEUM VERTEBRATE ZOOLOGY, 2593 LIFE SCIENCES BLDG., UNIV. CALIFORNIA, BERKELEY, CALIFORNIA 94720.) ACCEPTED 5 APR. 1979.

COLOR PLATE

The color plate Frontispiece of the Antarctic Petrel (*Thalassoica antarctica*) has been made possible by an endowment established by George Miksch Sutton. Joseph R. Jehl, Jr. provided the photograph.

Wilson Bull., 93(1), 1981, pp. 21–41

DISPLAY BEHAVIOR OF OVENBIRDS (*SEIURUS AUROCAPILLUS*) II. SONG VARIATION AND SINGING BEHAVIOR

M. Ross Lein

Song of the Ovenbird (*Seiurus aurocapillus*) is a characteristic sound of late spring and early summer in woodlands over much of North America. John Burroughs (1871) first used the onomatopoeic phrase teacher to describe its apparently double-syllabled phrases, characterizing it as a series of repetitions of this phrase, beginning softly and building in a crescendo. Although the Ovenbird was the subject of an intensive life-history study (Hann 1937) and of experimental investigations of song recognition (Weeden and Falls 1959, Falls 1963), there has been no detailed examination of song variation within local populations, or of the role of song in behavioral interactions.

In addition, the Ovenbird has a second song, often referred to as the "flight song," heard far less frequently than the normal teacher song. Many authors have commented on this display (Burroughs 1871, Gibbs 1885, Wright 1913, Allen 1919, Hann 1937, Kendeigh 1945), but it has not been described carefully on the basis of tape recordings and its significance has been largely a matter of speculation.

I previously have described the nature and use of non-song vocalizations of breeding Ovenbirds (Lein 1980). This paper describes the song variation of local populations, and documents singing behavior in detail.

METHODS

The study areas and methods are described in a previous paper (Lein 1980) and are summarized only briefly here. Fieldwork was conducted in 1970, 1971 and 1972 in Bedford, Middlesex Co., Massachusetts and in South Lyndeboro, Hillsboro Co., New Hampshire. The habitat consisted of second-growth mixed forest in both areas.

Detailed behavioral observations were made on 5–10 pairs of Ovenbirds each season, including 9 individually color-banded males. More casual observations were made on numerous other males. Individual males are identified by a 2-letter species designation (OB), plus a suffix designating the individual (OB-A, OB-B, etc.). Behavior was recorded on a cassette recorder and subsequently transcribed for analysis. Short-term singing rates (songs per min) were calculated from the time required for a bird to sing 10 complete songs, and were normally made only during regular singing not interrupted by other activity. Long-term singing rates (songs per h) during different phases of the breeding cycle were calculated from the number of songs males sang during entire observation periods. High-fidelity recordings of songs for audiospectrographic analysis were made with a Nagra IIIB tape recorder and a Norelco D-119ES cardioid dynamic microphone and analysed with a Kay Elemetrics 6061B audiospectrograph. Because of background noise and echos in recordings, I use trac-

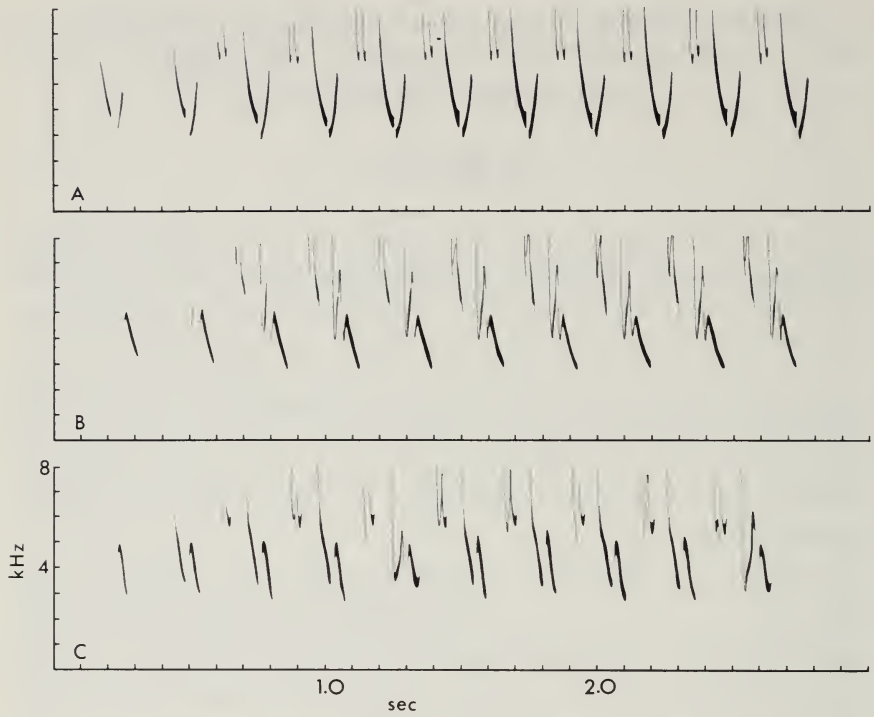


FIG. 1. Complete "primary songs" of male Ovenbirds: (A) song of OB-A; (B) song of OB-C; (C) song of an unbanded male. Note that the fifth and tenth phrases differ from the others: only 5 songs by this male, out of all songs recorded in this study, showed this phenomenon.

ings for illustration, rather than the actual sonagrams themselves. Terms describing the structure of the songs are used in the manner proposed by Shiovitz (1975).

RESULTS

Song variation

Male Ovenbirds have 2 vocalizations referred to as song: the normal "primary" or "territorial song" (Thorpe 1961), and the song referred to in the literature as the "flight song." This latter name is inappropriate because the vocalization is often given when the bird is not in flight. Therefore, I refer to this song as "attenuated song" and restrict the term "flight song" to those performed during a stereotyped aerial display (see below).

Primary Song

Description.—The "primary song" consists of a series of repetitions of a single phrase (Fig. 1A, B). Each phrase consists of 3–5 separate notes.

Most notes sweep rapidly downward in frequency with a concentration of energy between 3.0 and 5.0 kHz. The highest-pitched notes start at about 9.0 kHz and some notes may fall as low as 2.5 kHz. The phrases range in duration from 0.16–0.25 sec in different birds. The phrase is usually repeated from 8–13 times in complete songs. Songs longer than 14 phrases were heard only rarely, although once a song of 26 phrases was recorded. The phrases are separated by silent periods of about 0.05–0.1 sec. Complete songs vary in length from about 2.5–4.0 sec. Songs of an individual can vary considerably in length, however, depending on how many repetitions of the phrase are involved.

Although the first phrase of a song may be separated from the second by an interval longer than those occurring later in the song, the rate of delivery is usually constant after the second phrase. However, the amplitude increases for at least the first 5 or 6 phrases, producing the crescendo effect. The song is harsh and certainly could not be called musical, but it is delivered at such a loud volume that it carries long distances in the woods.

Intra-individual variation.—Each male Ovenbird sings a single phrase type. I recorded songs of 15 males repeatedly during this study (some over several years), and approximately 30 other males were recorded less regularly. Only once did a male sing more than 1 phrase pattern. On 24 May 1971, an unbanded male at Bedford sang 5 songs which included 1 or 2 phrases of a type other than the predominant one (Fig. 1C). This occurred about 5 min after a territorial encounter on the first day that the male was on territory. The significance of these circumstances is uncertain. All other songs of this male consisted of a single phrase type.

Complete songs of individuals showed minor variation in the number of phrases. For example, during 4 bouts of singing on 28 May 1971, OB-I sang 82 songs. These included songs with the following numbers of phrases: 7 phrases—1 song; 8 phrases—11 songs; 9 phrases—56 songs; 10 phrases—14 songs. Such variation was typical of all males, although the modal song length differed between birds.

Incomplete songs (arbitrarily defined as songs of less than 8 phrases) and muted songs were sung in a variety of situations described and analyzed in detail below. By definition, incomplete songs can vary from 1–7 phrases in length, but songs of 4 or 5 phrases predominated. Muted songs were delivered at a much lower volume than normal. Most incomplete songs are also muted since they are not long enough to develop the crescendo.

Inter-individual variation.—There is much inter-individual variation in the form of the phrases (Fig. 2). I did not attempt to sample all males over wide areas, but the samples from both Bedford (Fig. 2A-L) and South

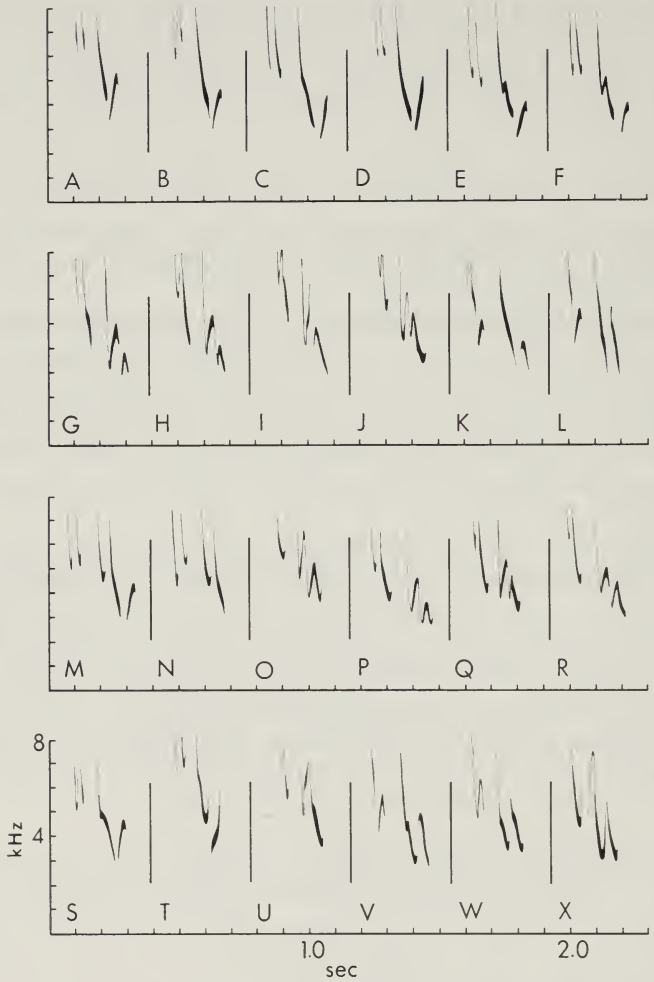


FIG. 2. Individual phrases from the "primary songs" of male Ovenbirds: (A–L) phrases from the songs of 12 males recorded at Bedford, Massachusetts: (M–X) phrases from the songs of 12 males recorded at South Lyndeboro, New Hampshire.

Lyndeboro (Fig. 2M-X) probably indicate the extent of variation within local populations.

In some cases, aural recognition of individuals was possible on the basis of the rate of delivery of the phrases or the quality of the phrases themselves. For example, OB-G (Fig. 2J) sang a recognizably more rapid song

than did his neighbors. Similarly, OB-I's song (Fig. 2L) was distinguishable to the ear by the squeaky quality of the phrases. Such aural discrimination could be made with certainty only for individuals with extremes of variation in these song characters.

The situation differs for audiospectrographic analysis. With a recording of reasonable quality I could always identify the singer by comparison with sonagrams of known individuals, even with males sharing a similar phrase structure and whose songs could not be distinguished reliably by ear. For example, OB-D (Fig. 2F) and OB-F (Fig. 2E) occupied neighboring territories. Their song phrases are very similar, but are characterized by a number of minor differences. The first 2 notes of OB-F's phrase terminate at a lower frequency than those of OB-D. The down-up-down inflection of the third note is more pronounced in OB-D's phrase. Finally, the terminal note of OB-F's phrase begins at a lower frequency than that of OB-D. Repeated recordings of these color-banded males established that these minor differences were constant and could be used to identify them. Similar consistent differences exist for other pairs of males with similar phrases (see OB-K and OB-J, Fig. 2Q, R).

Attenuated song

Description.—"Attenuated song" is a highly variable vocalization. Characteristically it is introduced by a series of *whink* notes and a *ple-bleep* vocalization (for a description of these calls see Lein 1980). Several normal song phrases occur immediately or shortly after the *ple-bleep*. This initial part of the song is followed by a rambling succession of other notes, many possessing a large amount of gradual frequency modulation (see Figs. 3 and 4). This "rambling" section of the song includes 1 or more *chip* notes and, in some examples, additional "primary song" phrases or *ple-bleep* notes. "Attenuated songs" are variable in length, ranging from 4–7 sec.

"Attenuated song" is frequently given as part of an aerial display, variously referred to as "love-song" (Burroughs 1871, Gross 1953), "passion song" (Jones 1900) and most frequently "flight song" (Chapman 1907, Hann 1937, Saunders 1951, Gross 1953, Gunn and Borror 1957). I use the last term to avoid the subjective implication of motivation.

"Flight song" was heard frequently and was recorded on a number of occasions. Because it was given irregularly, and most commonly at twilight, the performance was rarely seen. The male was initially perched in a tree, usually at the height of the subcanopy. The male gave a series of "soft sip" calls (Lein 1980) while perched. The rate of delivery of these calls accelerated until the bird took flight and climbed to 3–15 m above the treetops. He then flew in a hovering flight with spread wings and tail

while delivering the song. The flight appeared labored and the bird sometimes circled as it sang. Immediately upon completion of the song the bird dropped back into the woods.

"Attenuated song" was also frequently given by perched males during encounters with conspecifics. While the songs in such situations were often incomplete, they were frequently as long as those of the "flight song" display, and match the latter in form (Fig. 4B).

Intra-individual variation.—The "attenuated songs" of individuals vary within the constraints of the above description. In several cases, "flight songs" of the same individual recorded on different dates can be matched note by note throughout their entire length, indicating that there is some stereotypy in the form of the song. However, other examples of "flight songs" of the same male show differences in the rambling terminal portion, including variation in the ordering of the elements, repetition of some elements, or inclusion of a second series of phrases from "primary song" (Fig. 3A, B).

Inter-individual variation.—"Attenuated song" always includes 2 individually-distinctive elements: the *ple-bleep* vocalization (Lein 1980) and the "primary song" phrases. It is perhaps significant that both these elements occur together during the more stereotyped initial portion of the display. The terminal part of the song is more variable both within and between birds, but has the same quality and form in different males and there is much overlap in elements between birds (Figs. 3, 4).

Singing behavior

Primary song

General pattern of singing.—Singing is almost the only feature of Ovenbird biology that uses the vertical aspects of the territories. The Ovenbird is a ground-nesting, ground-foraging species and seldom perches in trees, except when singing or when alarmed. Prior to female arrival, undisturbed males sing regularly while sitting still on perches near the bottom of the canopy. Bouts of singing range from 1 or 2 to more than 20 min in length. The mean height (estimated within 1 m) of 95 Ovenbird song perches was 8.8 m (SE = ±0.23 m, range = 1.8–15.2 m), while the mean height of the trees in which they were perched was 15.5 m (SE = ±0.42 m, range = 3.0–24.5 m). Bouts of song are interspersed with bouts of feeding on the ground, during which males are silent, or sing very sporadically. Males feeding on the forest floor frequently would hop or flit up to a rock, stump or twig before singing one of these sporadic "ground" songs; then they would hop down and continue foraging. Several reasons may be suggested for the obvious reluctance of males to sing from the ground. First, singing

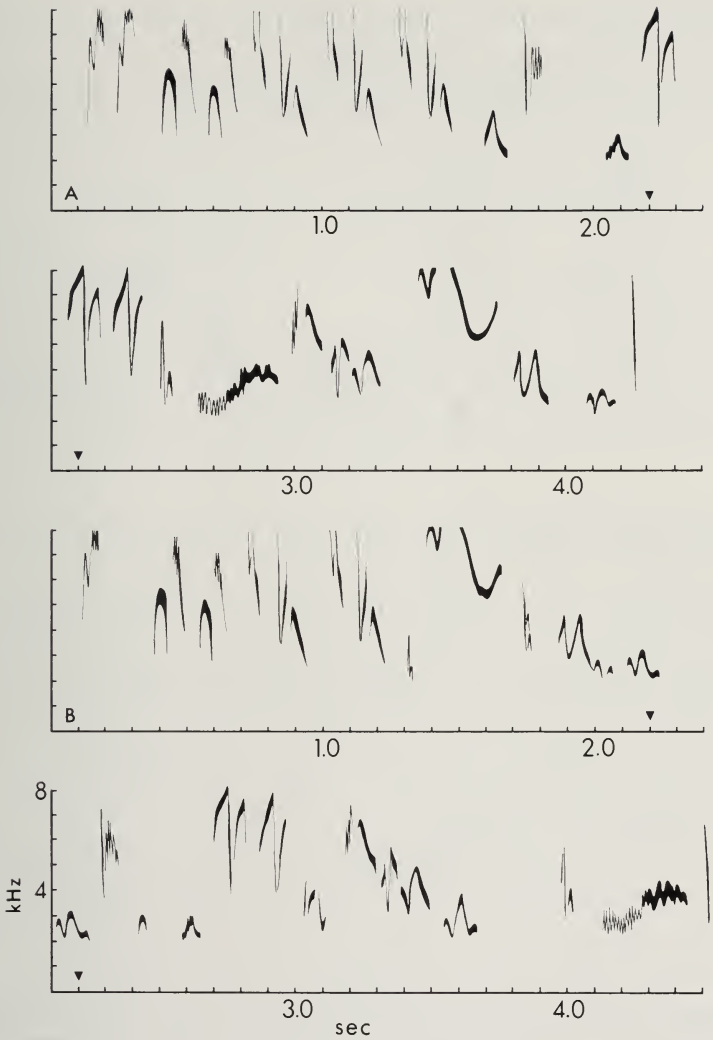


FIG. 3. "Attenuated songs" of male Ovenbirds, because of their length, have been broken for the illustrations. The solid triangles on the time axis indicate the point of overlap of the upper and lower portions of each song. (A–B) "Flight songs" of OB-C. Note the similar introduction of the 2 examples, consisting in A, of 2 *whink* calls, 1 *ple-bleep* call and 3 "primary song" phrases. Also note the occurrence of the same elements in different sequences in the terminal parts of the 2 examples.

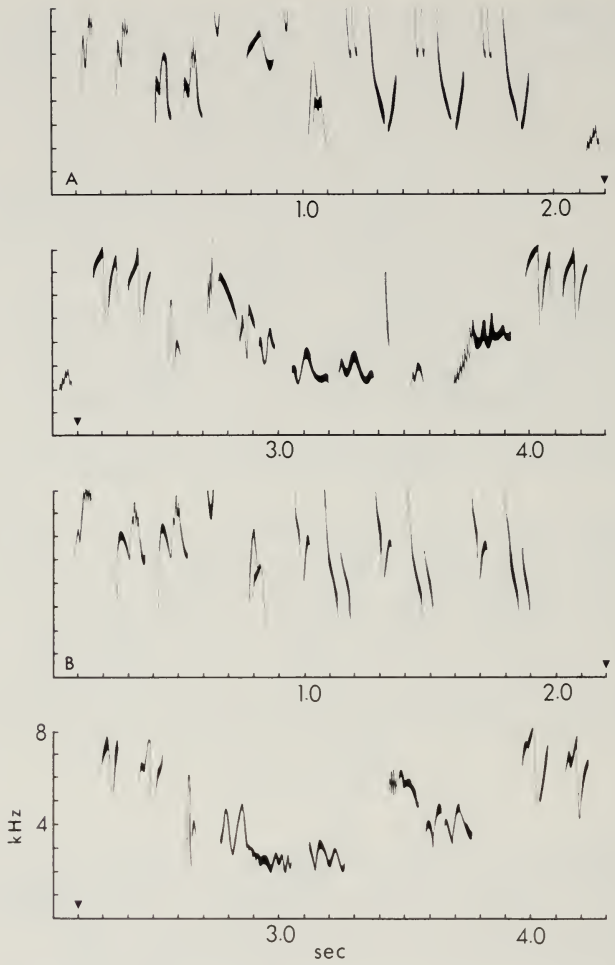


FIG. 4. "Attenuated Songs" of male Ovenbirds, because of their length, have been broken for the illustrations. ▼ on the time axis indicate the point of overlap of the upper and lower portions of each song. (A) "Flight song" of OB-A. Note the similarity of the elements to those of the "flight songs" of OB-C, shown in Fig. 3. (B) "Attenuated song" of OB-I given from the ground. Note the similarity in form to the "flight songs" illustrated in Fig. 3 and Fig. 4A.

on the ground may attract predators to an inconspicuously colored bird on the forest floor. Second, songs delivered from the ground may not carry well because of ground attenuation and interference by dense vegetation with sound transmission (Wiley and Richards 1978). Song perches are at a level of the vegetation profile which has an open structure, consisting

TABLE 1

SONG RATES OF MALE OVENBIRDS DURING STEADY SINGING IN RELATION TO OTHER FEATURES OF THE SITUATION[a]

Situation	Mean song rate[b] (songs/min ± SE)	Range (songs/min)	No. observations
Steady singing with no disturbance	3.20 ± 0.06	1.09–4.44	73
Steady singing with preening activity	2.80 ± 0.11	2.20–3.33	16
Counter-singing with another male	3.71 ± 0.12	2.98–4.41	12
Rapid singing in first morning bout[c]	4.24 ± 0.33	2.51–5.40	8
Rapid singing during territorial encounters[c]	6.36 ± 0.93	4.05–10.34	6

[a] Short-term song rates were calculated from the times required for 10-song intervals.

[b] Song rates differ significantly between situations (Model 1 one-way ANOVA, $P < 0.001$); rate for steady singing with no disturbance differs significantly from those for the other situations (Student-Newman-Keuls multiple range test, $P < 0.05$).

[c] Both these situations involve many incomplete and/or muted songs.

only of trunks and dead branches, with very few leaves and little shrubbery.

During the bouts of steady singing, Ovenbirds sing at a rate of about 3 or 4 songs per min (Table 1). Several features of the external situation influence the song rate. Bouts of intense preening activity result in a slightly slower rate, while several other factors, such as counter-singing with another male, increase the song rate (Table 1). In 2 situations in particular, during bouts of song at dawn, and during mild territorial encounters (and at the beginning and ending of more intense encounters), Ovenbirds may sing very rapidly. The highest rate recorded, 10.34 songs per min, occurred in such an encounter. However, in both of these situations, most of the songs given were incomplete and many were muted.

Counter-singing (Armstrong 1963) was noted frequently. Two neighboring males would sing in phase, the songs of 1 male following immediately after, or overlapping with, the songs of the leading male. Several facts suggest that this is not merely the fortuitous result of 2 males singing at approximately the same rate. First, the singing rate of such birds was higher than during normal singing (Table 1). Second, the relationship of "song a—song b—pause—song a—song b—pause . . ." could continue for 30–40 songs. When the relationship changed it was not due to the 2 birds drifting out of phase, as would be expected if it were fortuitous, but in many instances by the "b" bird not "waiting" for "song a," but rather singing his own song toward the end of the pause. In such cases, the birds would sometimes continue to counter-sing with the lead reversed. This demonstrates that the males are "paying attention" to the songs of neighboring males and responding to them, even at a considerable distance.

TABLE 2
LONG-TERM SINGING RATES OF MALE OVENBIRDS IN RELATION TO THE PHASE OF THE BREEDING CYCLE

Phase in cycle	No. observations[a]	Singing rate[b] (songs/h ± SE)	Observation time (min)
Unmated	21	139.4 ± 9.7	633
Courtship period	18	65.9 ± 10.2	692
Incubation period	13	85.4 ± 12.6	456
Nestling period	9	87.9 ± 13.7	299
Fledgling period and later	8	26.9 ± 5.8	296

[a] All observations during morning activity period.
[b] Singing rates differ significantly between phases of the breeding cycle (Model 1 one-way ANOVA, $P < 0.001$); rates for unmated and fledgling periods differ from those of other periods (Student-Newman-Keuls multiple range test, $P < 0.05$); rates for courtship, incubation and nestling period do not differ significantly.

Daily pattern of singing.—The effects of daily activity rhythms on singing behavior have been well-described (Thorpe 1961, Armstrong 1963). As in other birds, Ovenbirds show an activity peak in early morning and a second, smaller peak in the evening. The morning peak is more pronounced early in the breeding season, when the birds are very active until noon. Later in the season strong singing becomes more restricted to early hours. Extremely hot or cold weather inhibits singing, as does heavy rain. Early in the season, however, birds sing strongly during light rain.

Many workers have shown that the beginning of song at dawn, and to a lesser extent its cessation at dusk, is closely correlated with the light intensity (Armstrong 1963). The times of first songs of Ovenbirds gradually became earlier until the longest days of June, then became later as the summer progressed. A comparable relationship in the time of the last song of the evening was also noted.

Light intensity appears to influence singing in other ways as well. The songs at the beginning of the initial bouts of the morning were characteristically incomplete and/or muted. This was also true of late evening singing. Light level is also important in determining the occurrence of "flight song" (see below).

Seasonal pattern of singing.—A seasonal decline in singing is known for many species (Thorpe 1961, Armstrong 1963). Many studies have demonstrated that the long-term singing rates of a male bird are related not to the calendar date per se, but rather to the stage of the breeding cycle (see summary in Armstrong 1963:152–156). Since the breeding cycles of individual males are usually out of phase with one another, studies which report only population averages in relation to calendar date may miss important and abrupt changes.

The long-term singing rates of male Ovenbirds at various phases in the nesting cycle are shown in Table 2. All figures are based on observations made during the morning activity period (04:30–10:00 EDT). Unmated males sing an average of 139.4 songs per h. If they were singing at the mean rate calculated for undisturbed birds, 3.2 songs per min (Table 1), this would represent steady singing for about 75% of the time.

Upon arrival of females, however, singing rate drops significantly to 65.9 songs per h, a decrease of over 50%. The decline is related to the male's close association with the female at this time. During such activity he sings only sporadically and many of the songs are incomplete or muted, a feature rarely observed prior to female arrival.

Once incubation begins, the singing rate may increase slightly, but it never regains the level reached prior to mating. Song bouts are much more irregular during incubation and feeding of young. By early July regular singing is heard only for a short period at dawn.

Incomplete song.—The situations in which incomplete songs were used range from the occurrence of 1 or 2 incomplete songs during bouts of regular singing, to periods of up to 1 h when a male sang incomplete songs repeatedly while moving with his mate (Table 3). Half the observations involved association of paired males and females. Most of these were during courtship; contact between mates during the incubation or nestling periods is similar to that during courtship, although much less frequent or prolonged. Males used incomplete songs when at intermediate distances from their mates. When within 7 m or less of females, males rarely sang at all (with the exception of "attenuated song," see below). When more than 25–30 m from their mates, males usually sang full songs. Males changed from incomplete to full song (11 cases) as they moved away from their mates. Switching from full to incomplete song (7 cases), and from incomplete song to silence (9 cases), occurred as mates moved closer together. Males gave incomplete songs on 4 occasions in association with chases of their mates.

Incomplete songs were a regular feature of territorial encounters between males. Males gave incomplete songs at either a normal or a reduced and irregular rate during male-female interactions; during male-male encounters there frequently was an elevated rate of singing (Table 1). In some encounters, males sang incomplete songs almost continuously, with very short pauses between them. Incomplete songs were not used during intense interactions involving vigorous or prolonged chasing; these were characterized by silence or by the use of non-song vocalizations such as *chep*, *whink*, *ple-bleep* and *pink* (Lein 1980). Incomplete song was used during mild encounters, or at the beginning or end of encounters, or during pauses between bouts of active chasing.

TABLE 3
SUMMARY OF SITUATIONS IN WHICH MALE OVENBIRDS USED INCOMPLETE SONGS

Situation	No. cases	
	Major category	Subcategory[a]
Male-female interactions	49	
During association		49
During male-female chasing		4
Male-male interactions	15	
During territorial encounter		14
During male-male chasing		3
Response to approach of male		2
At territorial boundary		1
Non-encounter situations	34	
During dawn or dusk singing		27
While carrying food to young		2
During vigorous preening		3
At end of singing bout		2
Total	98	

[a] Total for subcategories may be greater than number of cases in major category since 1 observation may fall into several subcategories.

Birds also switched from full to incomplete songs in other circumstances. Several times a male began to sing incomplete songs when a neighbor, who had been silent or singing at a distance, suddenly approached the mutual territory boundary. Encounters did not ensue in these instances and the males resumed singing full songs when they separated. Once, a male switched to incomplete song when he moved near a known territorial boundary. The neighbor was not singing at the time although I had previously observed several territorial encounters in the same area. The bird resumed full song again when he moved away from the boundary.

Incomplete song was noted on 34 occasions not involving interactions. Twenty-seven cases occurred during the first bouts of song in the morning or during late evening singing. In view of the influence of light level on the onset or cessation of daily song, it is not surprising that the birds should show a transition from silence to incomplete song to full song during the morning twilight, or vice versa in the evening. An important difference was that the morning performance usually involved incomplete songs given very rapidly and regularly (Table 1), whereas the singing in the evening was typically slow and sporadic.

Other non-encounter circumstances in which incomplete song was used suggest that they were correlated with a conflict between a tendency to

TABLE 4
SUMMARY OF SITUATIONS IN WHICH MALE OVENBIRDS USED MUTED SONGS

Situation	No. cases	
	Major category	Subcategory[a]
Male-female interactions	19	
During association		19
During male-female chasing		2
Male-male interactions	10	
During territorial encounter		8
At territorial boundary		2
Non-encounter situations	4	
During dawn singing		2
While carrying food to young		1
Response to playback of song		1
Total	33	

[a] Total for subcategories may be greater than number of cases in major category since 1 observation may fall into several subcategories.

sing and a tendency to carry out some other activity. In 3 cases, males sang incomplete songs during vigorous preening while on a song perch; when the preening ceased, full song was resumed. Twice incomplete songs came at the end of a bout of full songs, just before the male ceased singing and began to forage. In 2 other instances, a male sang incomplete songs while foraging and carrying food to its young. Males were typically silent during this activity.

Muted songs.—Incomplete songs frequently sound muted, but since normal songs increase in volume for the first 4 or 5 phrases it is impossible to determine this with certainty. Therefore, only songs of 5 or more phrases are considered here. The situations in which muted songs were recorded (Table 4) are similar to those in which incomplete songs were employed (Table 3). Therefore, I will not consider the uses of muted song in detail. I believe that muted song is intermediate in motivation between incomplete song and full song, or that it represents a "less inhibited" variation of full song than does incomplete song. On several occasions, the first morning bout of singing of a male began with a series of incomplete (and certainly muted) songs. These gradually lengthened until they were recognizable as complete, but still muted, songs. Then there was a gradual increase in volume until the male was singing normal volume, full songs. I believe that this represents the usual pattern of onset of song in the morning, but I was rarely close enough to a singing male to ascertain that

Table 5
Distribution of Ovenbird Flight Songs by Time of Day

Beginning h[a]	No. displays[b]	Beginning h	No. displays
01:00	0	13:00	6
02:00	1	14:00	6
03:00	0	15:00	2
04:00	23	16:00	5
05:00	0	17:00	10
06:00	1	18:00	8
07:00	3	19:00	53
08:00	0	20:00	102
09:00	3	21:00	0
10:00	1	22:00	0
11:00	0	23:00	1
12:00	0	24:00	0

[a] All times are Eastern Daylight Time.
[b] Total of 225 displays recorded.

the intermediate songs were really muted. Similar transitions from full to muted to incomplete songs were occasionally noted at the beginning of male-male or male-female interactions; switching in these situations was often abrupt and frequently omitted 1 or more of the intermediate steps from full song to silence.

Attenuated song

Flight song.—I observed or heard 225 performances of the Ovenbird "flight song" display. There is a major concentration of displays at dusk (Table 5), with 155 (68.9%) occurring between 19:00 and 21:00. Most "flight songs" heard in an evening occurred in a 15–20 min interval when it was quite dark in the woods, although the sky was fairly bright and visibility was good in open areas. A second, smaller peak occurs at sunrise. Similar daily patterns of distribution of Ovenbird "flight songs" have been reported by Hann (1937) and Eaton (1957).

Because "flight songs" were noted in the course of other activities and there were no controlled observation periods, it is difficult to assess the remainder of the distribution pattern. The twilight peaks are so pronounced as to leave no question as to their reality. The rarity of "flight songs" during the morning is also real, since the majority of my fieldwork was between 05:00 and 11:00. "Flight songs" may occur at night (21:00–03:00) more frequently than recorded since almost no observations were made during this period.

TABLE 6

SUMMARY OF SITUATIONS IN WHICH MALE OVENBIRDS USED "ATTENUATED SONG" (EXCLUDING FLIGHT SONG)

Situation	No. cases	
	Major category	Subcategory[a]
Male-female interactions	17	
During association		17
During male-female chasing		6
During attack by male		2
During flight toward female		1
During copulation attempts		4
Male-male interactions	13	
During territorial encounter		13
During male-male chasing		6
After chasing		1
At end of encounter		1
Non-encounter situations	3	
At dawn or dusk		2
Late in breeding season		2
Total	33	

[a] Total for subcategories may be greater than number of cases in major category since 1 observation may fall into several subcategories.

The predisposing influence of low light intensity on the performance of "flight song" is evident from the twilight peaks. This is also suggested by the occurrence of "flight songs" during the middle of drizzly and heavily-overcast days. At least 9 (20%) of the 45 "flight songs" recorded between 06:00 and 19:00 occurred during such weather. On a dark afternoon, during light rain, I sometimes heard several "flight songs" in an hour. This never occurred during more clement weather.

Attenuated song during encounters.—Incomplete "attenuated songs" are often given, but all cases considered here included some of the "rambling" terminal portion of the song and may thus be considered to be complete. Of the 33 instances when "attenuated song" was recorded (excluding "flight song" performances), 30 involved interactions between conspecifics (Table 6). Its use in these situations is similar to those of incomplete and muted song, but with one difference. Twelve of 17 records during male-female interactions involved chases, aggressive (?) attacks by the male, or copulation attempts. This is a much higher association with very intense interaction than was recorded for incomplete or muted song (see Tables 3 and 4).

This association of "attenuated song" with high activity was also noted during male-male encounters. Almost half (6 of 13) of the records in territorial encounters were during aerial chases. This is in contrast to incomplete or muted songs which were rarely used during chases.

Attenuated song during non-encounter situations.—On 3 occasions, male Ovenbirds sang 1 or more "attenuated songs" from a perch, or from the ground, in the apparent absence of conspecifics (Table 6). Twice it occurred during the twilight of dusk or dawn when one might expect to hear "flight songs." The third record was somewhat different and warrants an extensive description.

On 7 July 1971, I was observing OB-I, who had been singing irregularly for at least 20 min. At 07:05 he flew down to the ground and in the next 4 min sang at least 16 "attenuated songs." All were muted in volume, but were full-length and had the form of other "attenuated songs" (Fig. 4B). Several times 2 or more of the songs were run together, so that the bird was singing the soft, rambling song for periods of 10–30 sec. This performance of "attenuated song" resembles what has been called "sub-song" (Thorpe 1961:64–70, Thorpe and Pilcher 1958, Armstrong 1963:58–69). Sub-song in other species is a low-volume, rambling vocalization, usually bearing little resemblance to the typical song, although it frequently contains call notes and isolated elements of "primary song." It may be produced almost continuously for extended periods of time. The similarity to the performance of OB-I is striking and suggests that a relationship may be involved.

DISCUSSION

Song variation.—The Ovenbird's pattern of song variation is a relatively simple one which is exhibited by many passerines (Borror 1961, Thielcke 1969). Each male possesses 1 "primary song" pattern, and the song patterns of different males in a local population show considerable variation. This is in contrast to the pattern shown by the Chestnut-sided Warbler (*Dendroica pensylvanica*) (Lein 1978) and some other members of that genus (Lein 1972; Morse 1966, 1967, 1970), in which each male possesses 2 or more song patterns shared by all males in a local population.

This type of individual song variation may facilitate individual recognition of neighbors' songs by male Ovenbirds. The experiments of Weeden and Falls (1959) clearly demonstrated that males discriminate between the songs of familiar and strange birds. The aggressive responses of males were more prompt and pronounced toward the songs of strangers. This implies that territorial establishment in this species results in a relatively stable relationship between neighbors. The outcome is that males are more tolerant toward neighbors, who presumably pose less of a threat to their

territorial security, than they are to strangers, who are likely to be newly-arrived birds searching for a territory. Subsequent work by Falls (1963) demonstrated that the pitch, form and arrangement of the component sounds of the song, and the length of the sounds and the intervals between them, are important in eliciting normal responses from male Ovenbirds during playback experiments. These are the features that vary between the songs of different individuals and they probably form the basis of individual discrimination.

The wide range of variation in phrase structure within a local population (Fig. 2), and the similarity of the phrases of some individuals in different populations (compare Fig. 2H and Q, and Fig. 2L and V), suggest that a system of "dialects" (Marler and Tamura 1962, Baptista 1975) is unlikely.

Little can be said regarding the pattern of variation in "attenuated song" because of the small sample of recordings. However, since it contains individually-distinctive "primary song" phrases and *ple-bleep* notes, it probably shows patterns of variation comparable to those of "primary song."

Singing behavior.—Several features of the singing behavior of Ovenbirds deserve comment, especially in relation to the differences found in a parallel study of the Chestnut-sided Warbler (Lein 1978). First, Ovenbirds rarely sing while foraging on the ground; Chestnut-sided Warblers commonly sing while foraging in foliage. Whatever the reasons for the Ovenbird's reluctance to sing from the ground, simultaneous singing and foraging are largely incompatible in this species. In contrast, the Chestnut-sided Warbler combines singing and foraging with only a slight decline in song rate (Lein 1978) and with little apparent interference with foraging. This difference has interesting consequences for time and energy budgets. If we assume, for the sake of argument, that males of both species require the same time and expend the same energy in acquiring the food necessary for subsistence, then it follows that Ovenbirds will have less time available for territorial proclamation than will Chestnut-sided Warblers. Although it is improbable that this assumption is strictly true, it suggests a manner in which the features of the foraging niche of the species could influence territorial advertisement. Species that can combine singing and foraging may be better suited to situations of intense territorial competition, or to conditions which require extended and continuous advertisement for other reasons.

The second difference is in the influence of pair formation on singing behavior. The large decline in singing of Ovenbirds at pairing is due to the almost continuous association of mates at this time, and its inhibitory effect on song. In contrast, pairing seems to have little influence on the singing of the Chestnut-sided Warbler, and perhaps on the singing of

sexually dimorphic warblers in general (Lein 1978, Morse 1966, Ficken and Ficken 1969). Chestnut-sided Warbler pairs spend relatively little time in association in the period between female arrival and the start of incubation (16.4% of 373 min of observations on birds whose exact breeding status was known) in contrast to the Ovenbird (83.4% of 452 min).

This sharp decline suggests that song functions in attracting females to unmated males. This is supported by the observation that males who lose their mates resume singing in a manner similar to that of newly-arrived males. However, because new males may be arriving and establishing territories after the first males are already mated, song probably continues to function in territorial proclamation and defense after pairing. The amount of time that a male Ovenbird devotes to pair-related activities during the courtship period possibly decreases his efficiency in territorial defense. Other males frequently intrude on a territory during the courtship period, but this may be due to the attractiveness of the highly vocal females to neighboring males at this time (pers. obs.) rather than to a decline in the efficiency of defense.

Communicative function of song.—The broad range of circumstances in which "primary song" is used indicates that, as with other Ovenbird vocalizations (Lein 1980), it encodes rather general behavioral messages (Smith 1969, 1977). It is rich in identifying messages, indicating that the singer is a male Ovenbird, in breeding condition and on his territory. In addition, a recipient with previous experience may be able to identify the singer as a specific individual. By monitoring singing rate over a period of time, the listener may also be able to determine the mating status of the singing male.

It is difficult to suggest which behavioral selection messages (Smith 1977) the signal encodes. Probably the message is one relating to interactional behavior, indicating that the singer is prepared to interact in any of the ways typical of territorial male Ovenbirds. This is perhaps the only behavioral selection message encoded. It could still have a variety of meanings to different recipients. To a male who was a potential intruder it could signify a threat; to an unmated female it could mean the presence of a potential mate.

Additional messages for muted or incomplete songs are equally difficult to determine. Although both variants are used in clearly agonistic situations, they also occur in circumstances not involving attack or escape, and hence these agonistic messages probably are not encoded. The only general feature of their use is that the bird is experiencing some type of inhibition of, or conflict with, his tendency to sing. Hence they may encode a message of indecisive behavior. This may provide information regarding

the communicator's probable future behavior, although the meanings of the signals are certainly dependent upon the class of recipient and the context. The frequent association of these variants with interactions suggests that they may encode a supplemental message indicating a greater probability of interaction than that of full "primary song."

"Attenuated song" used during interactions probably encodes information similar to that borne by incomplete or muted "primary song," since all these vocalizations are used in similar circumstances. In encounter situations "attenuated song" frequently accompanies chasing and attack. However, its use in other situations, such as copulation attempts and "flight song," argues against the encoding of a specific attack message. An attack meaning may be available to the recipient from the context of the signal. The main difference between the messages of "attenuated song" and muted or incomplete songs probably relates to differences in the supplemental messages of probability and intensity of the behavioral selection. "Attenuated song" may indicate a higher probability of a more intense interaction, either aggressive or sexual.

It seems impossible to assess the communicatory function of the "flight song," regardless of how dramatic it is. Its rare occurrence and peculiar situation of use, plus the obvious influence of low light level in its elicitation, make it difficult to suggest its function.

SUMMARY

Song variation and singing behavior of Ovenbirds were studied at 2 locations in New England. Each male possesses a single, distinctive "primary song," which may also be given in muted or incomplete forms. Males also possess a second type of song, "attenuated song," often used as part of an aerial display ("flight song").

Prior to pair formation, male Ovenbirds sing strongly from perches near the bottom of the forest canopy. Few songs are given from the ground, where the majority of foraging occurs. There is a sharp decline in singing at pairing, the result of the inhibitory effect of the female's presence on her mate's singing. Muted and incomplete "primary songs" are associated with both male-male and male-female interactions, but are used in other situations as well. "Flight song" is given primarily at dusk and dawn but may occur at other times, particularly during heavy overcast. Other performances of "attenuated song" are associated almost entirely with very intense interactions.

The relatively simple pattern of song variation described may facilitate individual recognition of neighbors' songs by males. The incompatibility of singing and foraging in this species suggests that features of the foraging niche may influence the ability of birds to advertise territories. Similarly, the reduction in singing produced by the extensive courtship interactions may affect the efficiency of territorial defense at this time.

The songs of Ovenbirds appear to be rich in the identifying messages they encode, but their message regarding future behavioral selections is probably very general, indicating only that the singer is prepared to interact in any manner typical of territorial male Ovenbirds. Muted and incomplete songs, and "attenuated songs," probably encode different supplemental messages about the probability and intensity of interaction.

ACKNOWLEDGMENTS

Professor Ernst Mayr supervised this study, and encouraged me in all its phases. He and Mrs. Mayr graciously allowed me to use their summer retreat in New Hampshire as a study area. W. John Smith provided valuable assistance with techniques and theoretical approaches to animal communication. M. S. Ficken and R. Zach improved the manuscript with their comments. Facilities and equipment were made available by the Museum of Comparative Zoology, Harvard University. Financial support was provided by Harvard University, the Carl A. and Katharine F. Richmond Fund, and National Science Foundation Grants GB7346 and GB19922 to Harvard University (R. C. Rollins, Principal Investigator).

LITERATURE CITED

Allen, F. H. 1919. The evolution of bird song. Auk 36:528–536.

Armstrong, E. A. 1963. A study of bird song. Oxford Univ. Press, London, England.

Baptista, L. F. 1975. Song dialects and demes in sedentary populations of the White-crowned Sparrow (*Zonotrichia leucophrys nuttalli*). Univ. Calif. Publ. Zool. 105:1–52.

Borror, D. J. 1961. Intraspecific variation in passerine bird songs. Wilson Bull. 73:57–78.

Burroughs, J. 1871. Wake-robin. Hurd and Houghton, New York, New York.

Chapman, F. M. 1907. The warblers of North America. D. Appleton and Co., New York, New York.

Eaton, S. W. 1957. A life history study of *Seiurus noveboracensis*. St. Bonaventure Univ., Sci. Stud. 19:7–36.

Falls, J. B. 1963. Properties of bird song eliciting responses from territorial males. Proc. 13th Int. Ornithol. Congr. 259–271.

Ficken, M. S. and R. W. Ficken. 1969. Responses of Blue-winged Warblers and Golden-winged Warblers to their own and the other species' song. Wilson Bull. 81:69–74.

Gibbs, M. 1885. Song of the Golden-crowned Thrush. (*Siurus auricapillus*). Ornithol. and Ool. 10:191–192.

Gross, A. O. 1953. Eastern Ovenbird. Pp. 457–476 *in* Life histories of North American wood warblers (A. C. Bent, ed.). U.S. Natl. Mus. Bull. 203.

Gunn, W. W. H. and D. J. Borror. 1957. Interpretations of some warbler songs. Pp. 26–36 *in* The warblers of America. (L. Griscom and A. Sprunt, Jr., eds.). Devin-Adair Co., New York, New York.

Hann, H. W. 1937. Life history of the Oven-bird in southern Michigan. Wilson Bull. 49:145–237.

Jones, L. 1900. Warbler songs (Mniotiltidae). Wilson Bull. 12:1–57.

Kendeigh, S. C. 1945. Nesting behavior of wood warblers. Wilson Bull. 57:145–164.

Lein, M. R. 1972. Territorial and courtship songs of birds. Nature 237:48–49.

———. 1978. Song variation in a population of Chestnut-sided Warblers (*Dendroica pensylvanica*): its nature and suggested significance. Can. J. Zool. 56:1266–1283.

———. 1980. Display behavior of Ovenbirds (*Seiurus aurocapillus*). I. Non-song vocalizations. Wilson Bull. 92:312–329.

Marler, P. and M. Tamura. 1962. Song "dialects" in three populations of White-crowned Sparrows. Condor 64:368–377.

Morse, D. H. 1966. The context of songs in the Yellow Warbler. Wilson Bull. 78:444–455.

———. 1967. The contexts of song in Black-throated Green and Blackburnian warblers. Wilson Bull. 79:64–74.

———. 1970. Territorial and courtship songs of birds. Nature 226:659–661.

Saunders, A. A. 1951. A guide to bird songs. Rev. Ed. Doubleday and Co., Inc. Garden City, New York.

Shiovitz, K. A. 1975. The process of species-specific song recognition by the Indigo Bunting, *Passerina cyanea*, and its relationship to the organization of avian acoustical behaviour. Behaviour 55:128–179.

Smith, W. J. 1969. Messages of vertebrate communication. Science 165:145–150.

———. 1977. The behavior of communicating. Harvard Univ. Press, Cambridge, Massachusetts.

Thielcke, G. 1969. Geographic variation in bird vocalizations. Pp. 311–339 *in* Bird vocalizations (R. A. Hinde, ed.). Cambridge Univ. Press, Cambridge, England.

Thorpe, W. H. 1961. Bird-song. Cambridge Univ. Press, Cambridge, England.

——— and P. M. Pilcher. 1958. The nature and characteristics of sub-song. Br. Birds 51:509–514.

Weeden, J. S. and J. B. Falls. 1959. Differential responses of male Ovenbirds to recorded songs of neighboring and more distant individuals. Auk 76:343–351.

Wiley, R. H. and D. G. Richards. 1978. Physical constraints on acoustic communication in the atmosphere: implications for the evolution of animal vocalizations. Behav. Ecol. Sociobiol. 3:69–94.

Wright, H. W. 1913. Morning awakening and even-song. Second paper. Auk 30:512–537.

dept. biology, univ. calgary, calgary, alberta t2n 1n4 canada. accepted 2 aug. 1979.

MEANDARRA ORNITHOLOGICAL FIELD STUDY UNIT

In December 1980 the Meandarra Ornithological Field Study Unit (MOFSU) was formally established as a research group of the University of Queensland, Australia. Active in field research mainly near Meandarra, 300 km west of Brisbane, MOFSU's major interest is in aspects of the behavior and ecology of communally breeding species. Visitors and volunteer field assistants are welcomed, and although no funding is available, students are accepted to work on field projects towards an M.Sc. or Ph.D. For further information write to: Dr. Douglas Dow, Director, MOFSU, Dept. Zoology, University of Queensland, Brisbane, Australia, 4067.

INTERNATIONAL COMMISSION ON ZOOLOGICAL NOMENCLATURE

The following opinion has been published by the ICZN in the Bulletin of Zoological Nomenclature, Vol. 38, Pt. 1, 26 Feb. 1981: Opinion No. 1168 (p. 69) "*Cacatua ducorpsii* Pucheran, 1853 (Aves): conserved." The Commission cannot supply separates of Opinions.

Wilson Bull., 93(1), 1981, pp. 42–53

THE MAYFIELD METHOD OF ESTIMATING NESTING SUCCESS: A MODEL, ESTIMATORS AND SIMULATION RESULTS

Gary L. Hensler and James D. Nichols

Mayfield (1960, 1961, 1975) proposed a method of estimating nesting success which removes potential sources of bias often associated with other estimates of this parameter. Despite the intuitive appeal of Mayfield's method and the general recognition that it is appropriate (e.g., Miller and Johnson 1978, Custer and Pitelka 1977, Johnson 1979), it is still not widely used. In this paper we present a probabilistic model for the experimental situation considered by Mayfield (1960, 1961, 1975). We then obtain maximum likelihood estimators based on this model and present results of Monte Carlo simulations designed to evaluate the estimators. Sample size considerations are also discussed.

Mayfield's method is based on the concept of "nest days." The model he employs assumes the following: (a) the complete period to success, which we will call the nesting period, (for example, the period of incubation of eggs) is the same number of days, say J days, for all nests; (b) there is a constant unknown probability, p ($0 < p < 1$), over this period that a nest observed on day j will survive to day j + 1; the probability of a nest succeeding from day 1 to full term is then p^J; (c) there is a fixed unknown probability, θ_j, that an observed nest will have been first found on day j of the nesting period of J days (for j = 1, 2, . . . , J).

Assume that we observe K nests under the above model. For each of these nests we observe a random vector $X_k = (Y_k, T_k)$, k = 1, 2, . . . , K, where (i) Y_k is a random variable taking the value 1 if the kth nest is successful (i.e., survives the complete nesting period) and the value 0 if the nest fails at any time, and (ii) T_k is a random variable denoting the number of days the kth nest is observed until it either succeeds or fails. For example, an observation of (0, 10) would mean a nest was seen on 10 days but on the 11th day visit it had failed, while a value of (1, 10) would mean a nest was seen on 10 days and on the 11th day was observed to have succeeded (for example, hatchlings were present on day 11). Given the random vectors $X_1, \ldots, X_k$ we wish to estimate p, the daily probability of survival.

To do this we consider the joint distribution of (Y_k, T_k):

$$f(y, t \mid p) = [\theta_{J-t+1} p^t]^y \left[p^{t-1}(1 - p) \sum_{j=1}^{J-t+1} \theta_j \right]^{1-y} \quad (1)$$

Table 1

Results of Monte Carlo Simulations Designed to Evaluate the Maximum Likelihood Estimators for Daily Survival Probability and Its Variance[a]

J	p	p^J	1/I(p)	K	Mean estimated values					Max $\hat{p}$	Min $\hat{p}$	Actual confidence interval coverage		
					$\hat{p}$	$\hat{p}^J$	$\hat{v}$	$K\hat{v}^2$	$\bar{Y}$			90%	95%	99%
10				20	0.741	0.050	0.0536	0.0586	0.152	0.850	0.526	0.90	0.95	0.99
	0.750			75	0.750	0.056	0.0270	0.0551	0.152	0.843	0.688	0.91	0.95	0.99
		0.056		500	0.751	0.057	0.0105	0.0548	0.152	0.773	0.728	0.92	0.95	1.00
			0.0551											
10				20	0.849	0.195	0.0387	0.0307	0.369	0.931	0.750	0.93	0.96	0.98
	0.850			75	0.846	0.188	0.0204	0.0315	0.363	0.890	0.789	0.87	0.91	1.00
		0.197		500	0.849	0.195	0.0078	0.0305	0.367	0.873	0.827	0.89	0.94	0.97
			0.0302											
10				20	0.901	0.353	0.0308	0.0197	0.547	0.972	0.750	0.87	0.94	0.96
	0.900			75	0.899	0.345	0.0161	0.0198	0.539	0.936	0.855	0.87	0.94	0.99
		0.349		500	0.902	0.357	0.0062	0.0190	0.539	0.915	0.886	0.89	0.94	0.99
			0.0194											
10				20	0.947	0.580	0.0221	0.0103	0.739	0.989	0.896	0.90	0.94	0.97
	0.950			75	0.952	0.611	0.0109	0.0090	0.758	0.974	0.919	0.84	0.92	0.98
		0.599		500	0.950	0.599	0.0043	0.0095	0.744	0.959	0.938	0.95	0.98	1.00
			0.0094											
20				20	0.847	0.036	0.0336	0.0231	0.131	0.913	0.736	0.93	0.95	0.98
	0.850			75	0.847	0.036	0.0173	0.0225	0.120	0.890	0.799	0.93	0.97	0.99
		0.039		500	0.850	0.039	0.0066	0.0218	0.122	0.864	0.830	0.93	0.95	0.99
			0.0218											
20				20	0.899	0.119	0.0251	0.0132	0.288	0.957	0.754	0.83	0.88	0.96
	0.900			75	0.899	0.119	0.0129	0.0127	0.277	0.929	0.862	0.89	0.92	0.99
		0.122		500	0.901	0.124	0.0050	0.0123	0.280	0.912	0.885	0.88	0.93	0.96
			0.0124											

TABLE 1
CONTINUED

J	p	p^J	1/I(p)	K	Mean estimated values $\hat{p}$	$\hat{p}^J$	$\hat{v}$	$K\hat{v}^2$	$\bar{Y}$	Max $\hat{p}$	Min $\hat{p}$	Actual confidence interval coverage 90%	95%	99%
20				20	0.948	0.344	0.0166	0.0058	0.554	0.980	0.903	0.84	0.90	0.96
	0.950			75	0.949	0.351	0.0086	0.0056	0.558	0.967	0.928	0.90	0.95	0.99
		0.358		500	0.950	0.358	0.0033	0.0055	0.558	0.958	0.943	0.89	0.94	1.00
			0.0054											
20				20	0.969	0.533	0.0125	0.0033	0.712	0.995	0.931	0.91	0.95	0.98
	0.970			75	0.970	0.544	0.0064	0.0032	0.715	0.985	0.957	0.91	0.96	0.97
		0.544		500	0.970	0.544	0.0025	0.0030	0.718	0.976	0.965	0.90	0.95	1.00
			0.0031											
20				20	0.991	0.835	0.0066	0.0010	0.913	1.000	0.973	0.79	0.84	1.00
	0.990			75	0.990	0.818	0.0035	0.0010	0.900	0.998	0.982	0.92	0.95	0.98
		0.818		500	0.990	0.818	0.0014	0.0010	0.898	0.993	0.987	0.90	0.97	0.99
			0.0010											
30				20	0.893	0.034	0.0240	0.0119	0.129	0.953	0.820	0.89	0.95	0.99
	0.900			75	0.899	0.041	0.0118	0.0106	0.135	0.927	0.860	0.89	0.93	0.97
		0.042		500	0.900	0.042	0.0045	0.0103	0.131	0.910	0.891	0.92	0.98	1.00
			0.0104											
30				20	0.948	0.201	0.0146	0.0044	0.398	0.978	0.895	0.90	0.93	0.98
	0.950			75	0.949	0.208	0.0074	0.0042	0.403	0.971	0.930	0.86	0.88	0.98
		0.215		500	0.950	0.215	0.0028	0.0040	0.411	0.957	0.942	0.91	0.97	0.99
			0.0040											
30				20	0.968	0.377	0.0109	0.0025	0.594	0.997	0.944	0.93	0.96	0.98
	0.970			75	0.969	0.389	0.0055	0.0023	0.600	0.981	0.952	0.90	0.94	0.99
		0.401		500	0.970	0.401	0.0021	0.0022	0.603	0.976	0.964	0.90	0.95	0.98
			0.0022											

TABLE 1
CONTINUED

J	p	p^J	1/I(p)	K	Mean estimated values					Max $\hat{p}$	Min $\hat{p}$	Actual confidence interval coverage		
					$\hat{p}$	$\hat{p}^J$	$\hat{v}$	$K\hat{v}^2$	$\bar{Y}$			90%	95%	99%
30				20	0.990	0.740	0.0058	0.0007	0.848	1.000	0.969	0.79	0.86	0.97
	0.990			75	0.990	0.740	0.0029	0.0007	0.857	0.997	0.982	0.87	0.91	0.96
		0.740		500	0.990	0.740	0.0011	0.0007	0.854	0.993	0.987	0.86	0.90	0.96
			0.0007											
30				20	0.995	0.860	0.0043	0.0004	0.925	1.000	0.984	0.96	0.99	1.00
	0.995			75	0.995	0.860	0.0021	0.0003	0.925	0.999	0.986	0.88	0.91	0.93
		0.860		500	0.995	0.860	0.0008	0.0003	0.925	0.997	0.993	0.88	0.95	0.99
			0.0003											
40				20	0.949	0.123	0.0132	0.0036	0.293	0.972	0.905	0.89	0.95	0.91
	0.950			75	0.950	0.129	0.0067	0.0034	0.301	0.963	0.933	0.90	0.96	1.00
		0.129		500	0.950	0.129	0.0026	0.0034	0.294	0.955	0.942	0.87	0.92	0.99
			0.0034											
40				20	0.967	0.261	0.0098	0.0020	0.482	0.989	0.942	0.91	0.93	0.97
	0.970			75	0.969	0.284	0.0049	0.0018	0.503	0.981	0.955	0.87	0.93	0.98
		0.296		500	0.970	0.296	0.0019	0.0018	0.507	0.974	0.967	0.95	0.98	1.00
			0.0018											
40				20	0.990	0.669	0.0055	0.0011	0.806	1.000	0.971	0.86	0.88	0.95
	0.990			75	0.990	0.669	0.0026	0.0005	0.811	0.996	0.983	0.87	0.96	0.98
		0.669		500	0.990	0.669	0.0010	0.0005	0.805	0.992	0.987	0.88	0.96	0.99
			0.0005											
40				20	0.995	0.818	0.0096	0.0064	0.898	1.000	0.984	0.99	1.00	1.00
	0.995			75	0.995	0.818	0.0018	0.0003	0.903	0.999	0.989	0.83	0.90	0.95
		0.818		500	0.995	0.818	0.0007	0.0003	0.901	0.996	0.993	0.91	0.94	1.00
			0.0003											

[a] All estimates are based on 100 simulations. J represents the entire nesting period; p and $\hat{p}$ are the true and estimated values of daily survival probability; p^J and $\hat{p}^J$ are the true and estimated probabilities of a new nest surviving the entire nesting period and succeeding; 1/I(p) and $K\hat{v}^2$ are the true and estimated variances of $\sqrt{K}\,(\hat{p}\text{-}p)$; $\sqrt{1/KI(p)}$ and $\hat{v}$ are the true and estimated asymptotic standard deviations of $\hat{p}$; K denotes the number of nests observed; $\bar{Y}$ denotes the observed proportion of nests which is successful.

$$\text{for} \quad y = 0, 1 \quad \text{and} \quad t = 1, 2, \ldots, J.$$

The log likelihood function (see Cramér 1946:498–506) for our random sample is:

$$\begin{aligned} &\log \prod_{k=1}^{K} \left[\theta_{J-T_k+1}\right]^{Y_k} + \left[\sum_{k=1}^{K} T_k Y_k\right] \log p \\ &+ \sum_{k=1}^{K} (T_k - 1)(1 - Y_k) \log p + \left(K - \sum_{k=1}^{K} Y_k\right) \log(1 - p) \\ &+ \log \prod_{k=1}^{K} \left[\sum_{j=1}^{J-T_k+1} \theta_j\right]^{1-Y_k}. \end{aligned} \tag{2}$$

Differentiating (2) with respect to p, setting the derivative equal to zero and solving for p, yields the maximum likelihood estimate (m.l.e.) of p, say $\hat{p}$ (see Cramér 1946:498–506). Here we have

$$\hat{p} = \frac{\sum_{k=1}^{K} T_k + \sum_{k=1}^{K} Y_k - K}{\sum_{k=1}^{K} T_k}. \tag{3}$$

Mayfield (1960, 1961, 1975) proposes the following estimator for p: Count the total number of nest days observed $\left(\text{i.e., } \sum_{k=1}^{K} T_k\right)$; count the total number of failures $\left(\text{i.e., } K - \sum_{k=1}^{K} Y_k\right)$, and estimate p by $1 - \dfrac{K - \sum_{k=1}^{K} Y_k}{\sum_{k=1}^{K} T_k}$ which is in fact $\hat{p}$, the m.l.e.

The theory of maximum likelihood yields that the asymptotic distribution of $\sqrt{K}\,(\hat{p} - p)$ is Normal with mean zero and variance $1/I(p)$ where $I(p)$ is the Fisher information and

$$I(p) = -E\left[\frac{\partial^2 \log f(Y, T \mid p)}{\partial p^2}\right]$$

(see Cramér 1946:498–506). As usual, E denotes expected value. Thus, the asymptotic variance of $\hat{p}$ is

$$\frac{1}{K\, I(p)} = \frac{1}{K} \frac{p^2(1 - p)^2}{ET(1 - p)^2 + (EY - 1)(1 - 2p)} \tag{4}$$

which we can estimate as

$$\hat{v}^2 = \begin{cases} \dfrac{\dfrac{1}{(K)}\hat{p}^2(1-\hat{p})^2}{\bar{T}(1-\hat{p})^2 + (\bar{Y}-1)(1-2\hat{p})} = \dfrac{\hat{p}(1-\hat{p})}{K\,\bar{T}} & \text{if} \quad \bar{Y} \neq 1 \\ \dfrac{1}{K\,\bar{T}} & \text{if} \quad \bar{Y} = 1. \end{cases}$$

Here $\bar{T}$ and $\bar{Y}$ denote the sample means of T and Y, respectively. Approximate $1 - \alpha$ confidence intervals for p are then given by

$$(\hat{p} - z_{\alpha/2}\hat{v},\ \hat{p} + z_{\alpha/2}\hat{v})$$

where $z_{\alpha/2}$ is the upper $\alpha/2$ value for the standard normal distribution,

$$\text{i.e.,} \quad \int_{-\infty}^{z_{\alpha/2}} \frac{1}{\sqrt{2\pi}} \exp(-z^2/2)\, dz = 1 - \alpha/2.$$

Similarly, approximate level α tests for the equality of p values from 2 populations of nests are given by the following: reject H_0, the null hypothesis that $p_1 = p_2$, in favor of the alternative hypothesis that $p_1 \neq p_2$ if and only if

$$(5) \qquad \frac{|\hat{p}_1 - \hat{p}_2|}{\sqrt{\hat{v}_1^2 + \hat{v}_2^2}} > z_{\alpha/2}.$$

The behavior of these confidence intervals and tests depends on the efficacy of $\bar{T}$, $\bar{Y}$, and $\hat{p}$ as estimators of ET, EY and p respectively. To investigate this behavior we performed Monte Carlo simulations of a nesting experiment which met the assumptions of our model. We chose several values of J (nesting period), K (the number of observed nests) and p (the daily survival probability). The θj probabilities were chosen to be in proportion to the available number of nests from the jth day of nesting given that the same number of new nests are started each day and only p of them survive to the second day, p^2 to the third, etc.; i.e.,

$$\text{we set } \theta_j = \frac{p^{j-1}(1-p)}{1-p^J}, \quad j = 1, 2, \ldots, J.$$

We randomly divided the K nests into J groups using the distribution given by the θ_j values. Each nest from the jth group was then followed until it survived for $J - j + 1$ days or until it failed. The probability of daily survival was p, and the probability of full term success for a nest for J days was p^J. The appropriate (Y,T) vector was recorded for each of the K nests, and $\hat{p}$, $\hat{v}$, and estimated confidence intervals (90%, 95%, 99%) were calculated. It was then determined whether or not the computed

TABLE 2

RESULTS OF SIMULATIONS INVESTIGATING THE POWER OF THE SUGGESTED TEST STATISTIC, $|\hat{p}_1 - \hat{p}_2| / \sqrt{\hat{v}_1^2 + \hat{v}_2^2}$[a]

J	p_1	K	Δ												
			−0.040	−0.030	−0.020	−0.010	−0.005	−0.001	0.0	0.001	0.005	0.010	0.020	0.030	0.040
			Proportion of the times null hypothesis was rejected at the ($\alpha = 0.10$, $\alpha = 0.05$, $\alpha = 0.01$) significance levels												
10	0.95	20	0.37	0.23	0.16	0.14	0.13	0.08	0.09	0.09	0.09	0.13	0.15	0.30	0.31
			0.21	0.13	0.07	0.04	0.06	0.03	0.06	0.03	0.05	0.06	0.05	0.12	0.16
			0.07	0.06	0.01	0.00	0.00	0.00	0.01	0.00	0.01	0.01	0.00	0.01	0.01
		75	0.77	0.45	0.37	0.17	0.11	0.10	0.09	0.19	0.11	0.15	0.48	0.80	0.93
			0.69	0.33	0.25	0.10	0.06	0.05	0.04	0.11	0.05	0.09	0.32	0.70	0.89
			0.45	0.14	0.09	0.03	0.01	0.00	0.00	0.04	0.01	0.02	0.05	0.38	0.78
		500	1.00	1.00	0.91	0.43	0.26	0.07	0.08	0.08	0.25	0.56	0.99	1.00	1.00
			1.00	0.99	0.86	0.35	0.15	0.01	0.04	0.02	0.14	0.38	0.98	1.00	1.00
			1.00	0.95	0.67	0.11	0.04	0.00	0.01	0.00	0.07	0.18	0.88	1.00	1.00
20	0.95	20	0.40	0.34	0.19	0.10	0.11	0.05	0.06	0.10	0.07	0.14	0.32	0.42	0.76
			0.26	0.24	0.13	0.06	0.07	0.00	0.02	0.08	0.05	0.06	0.21	0.30	0.67
			0.10	0.09	0.02	0.00	0.02	0.00	0.00	0.00	0.01	0.01	0.04	0.09	0.26
		75	0.88	0.70	0.46	0.17	0.15	0.06	0.11	0.12	0.10	0.21	0.60	0.92	0.99
			0.82	0.58	0.38	0.10	0.10	0.04	0.03	0.06	0.04	0.10	0.48	0.92	0.99
			0.57	0.29	0.16	0.03	0.03	0.00	0.00	0.00	0.02	0.02	0.28	0.75	0.96
		500	1.00	1.00	0.99	0.61	0.28	0.10	0.11	0.09	0.35	0.74	1.00	1.00	1.00
			1.00	1.00	0.99	0.50	0.19	0.09	0.04	0.05	0.28	0.68	0.99	1.00	1.00
			1.00	1.00	0.92	0.26	0.08	0.01	0.01	0.02	0.06	0.37	0.99	1.00	1.00

TABLE 2
CONTINUED

J	p_1	K	Δ −0.040	−0.030	−0.020	−0.010	−0.005	−0.001	0.0	0.001	0.005	0.010	0.020	0.030	0.040
30	0.95	20	0.54	0.34	0.28	0.08	0.07	0.07	0.09	0.11	0.11	0.18	0.37	0.57	0.83
			0.33	0.23	0.15	0.05	0.03	0.03	0.06	0.07	0.07	0.12	0.21	0.47	0.80
			0.10	0.07	0.02	0.00	0.01	0.00	0.01	0.01	0.02	0.00	0.09	0.22	0.55
		75	0.96	0.78	0.58	0.25	0.08	0.08	0.11	0.03	0.19	0.33	0.79	0.98	1.00
			0.88	0.70	0.39	0.17	0.04	0.01	0.07	0.02	0.09	0.18	0.65	0.98	1.00
			0.66	0.40	0.19	0.05	0.00	0.00	0.03	0.01	0.01	0.06	0.37	0.88	1.00
		500	1.00	1.00	0.99	0.74	0.27	0.07	0.14	0.09	0.34	0.88	1.00	1.00	1.00
			1.00	1.00	0.99	0.69	0.20	0.02	0.08	0.07	0.23	0.83	1.00	1.00	1.00
			1.00	1.00	0.98	0.43	0.09	0.00	0.03	0.00	0.11	0.64	1.00	1.00	1.00
40	0.99	20	0.94	0.81	0.66	0.36	0.14	0.10	0.09	0.11	0.09	—[b]	—	—	—
			0.90	0.73	0.49	0.24	0.07	0.01	0.03	0.05	0.03	—	—	—	—
			0.66	0.39	0.21	0.03	0.02	0.00	0.01	0.00	0.00	—	—	—	—
		75	1.00	1.00	0.98	0.66	0.29	0.15	0.09	0.11	0.39	—	—	—	—
			1.00	1.00	0.97	0.55	0.20	0.06	0.05	0.05	0.29	—	—	—	—
			1.00	0.99	0.87	0.31	0.04	0.01	0.02	0.02	0.17	—	—	—	—
		500	1.00	1.00	1.00	1.00	0.95	0.15	0.15	0.24	1.00	—	—	—	—
			1.00	1.00	1.00	1.00	0.87	0.09	0.08	0.16	1.00	—	—	—	—
			1.00	1.00	1.00	1.00	0.69	0.03	0.01	0.05	0.94	—	—	—	—

[a] 100 simulations were conducted for each combination of J, p_1, K and Δ values. In each simulation, 2 groups of nests characterized by p_1 and p_2 (where $p_2 = p_1 + \Delta$) were sampled and $\hat{p}_1$, $\hat{v}_1$, $\hat{p}_2$ and $\hat{v}_2$ estimated. The proportion of these simulations in which the null hypothesis ($p_1 = p_2$) is rejected is presented (for $\Delta = 0$ this estimates the significance level of the test). J denotes the nesting period and K is the number of nests observed for both of the simulated groups. Results are presented for 3 significance levels ($\alpha = 0.10, 0.05, 0.01$) for each set of simulations.

[b] For $p_1 = 0.99$, values of $\Delta \geq 0.01$ are not biologically reasonable. Thus, values for $\Delta \geq 0.01$ are not presented.

confidence intervals contained the true value of p. The entire above procedure was repeated 100 times for each combination of J, p and K values. We computed the proportion of the 100 times in which the estimated confidence interval in fact covered the true value. We also determined the mean, minimum and maximum values of the 100 estimates of p, the mean value of the 100 estimates $\hat{v}$ and the mean of the 100 estimates $K\hat{v}^2$ (which should estimate 1/I(p)). These values are compared with the theoretical values, p, 1/I(p), and the exact confidence proportions, in Table 1. The means of the estimated values $\hat{p}$ and $K\hat{v}^2$ appeared to be good estimators of p and 1/I(p) in virtually all simulated cases. In addition, the actual confidence interval coverages were close to the theoretical values, especially when it is remembered that proportions represent results of only 100 simulations.

We also calculated $\hat{p}^J$ as an estimate of $p^1 = p^J$, the probability of full term success. An alternative estimate of p^1, which is commonly used in nesting studies, is $\bar{Y} = \sum_{k=1}^{K} Y_k/K$, the ratio of the number of observed successful nests to total observed nests. The comparisons of $\hat{p}^J$ and $\bar{Y}$ as estimates of p^1 show the superiority of $\hat{p}^J$ in cases where the model assumptions are met (Table 1).

All of the results presented in Table 1 were obtained assuming

$$\theta_j = \frac{p^{j-1}(1 - p)}{1 - p^J}, \quad j = 1, 2, \ldots, J.$$

In order to assess the robustness of the above procedures to changes in this assumption we set all θ_j equal (i.e., $\theta_j = 1/J$, $j = 1, 2, \ldots, J$) and conducted additional simulations for many of the situations examined in Table 1. Results were virtually identical to those presented in Table 1, indicating that the estimators are quite robust with respect to reasonable changes in the θ_j values.

In addition, we ran Monte Carlo simulations of tests of equality of two p values using the test statistic in (5). We assessed both type I and type II error probabilities under several experimental situations. These results are presented in Table 2 and can be used as empirical approximations to the power of these hypothesis tests under various conditions. It should be noted that the power curve is not symmetric. Thus, for a specified value of Δ a test of the null hypothesis that $p_1 = p_2$ given that $p_2 = p_1 + \Delta$ (for $p_1 > 0.5$) is more powerful for $\Delta > 0$ than for $\Delta < 0$.

We note that the estimator $\hat{v}^2$ can be useful in planning an experiment in which the daily survival probability is to be estimated. If we express the desired precision of $\hat{p}$ in terms of a specific coefficient of variation, cv (where cv = v/p), then we can substitute estimates or guesses for p, ET, EY

TABLE 3

SAMPLE SIZES (NUMBER OF NESTS) NEEDED TO ESTIMATE DAILY SURVIVAL PROBABILITY (p) WITH SPECIFIED LEVELS OF PRECISION[a]

Nesting period (J)	Daily survival probability (p)	Desired coefficient of variation (v/p)					
		0.050	0.040	0.030	0.020	0.010	0.005
		Sample size					
10	0.75	39	61	109	245	980	3918
10	0.85	—	26	47	105	419	1675
10	0.90	—	—	27	60	239	957
10	0.95	—	—	—	26	104	415
20	0.85	—	—	34	75	301	1205
20	0.90	—	—	—	38	154	615
20	0.95	—	—	—	—	60	239
20	0.97	—	—	—	—	33	130
20	0.99	—	—	—	—	—	40
30	0.90	—	—	—	32	128	513
30	0.95	—	—	—	—	45	178
30	0.97	—	—	—	—	23	93
30	0.99	—	—	—	—	—	27
40	0.95	—	—	—	—	37	149
40	0.97	—	—	—	—	—	75
40	0.99	—	—	—	—	—	21

[a] Sample sizes were computed from (6). Values less than 20 were not presented, because we do not believe it is appropriate to recommend such small sample sizes. Reasons for this belief are: (1) we question the applicability of results relying on asymptotic theory to such small sample sizes; and (2) since (6) involves guesses of p, ET and EY, we feel the resulting uncertainty would never warrant our recommending a sample size of less than 20 nests.

(denote these guesses by p^*, $\bar{T}^*$, $\bar{Y}^*$) into (4) and obtain the approximate number of nests, K^*, we need to observe:

$$K^* = \frac{(1 - p^*)^2}{\bar{T}^*(1 - \hat{p})^2 + (\bar{Y}^* - 1)(1 - 2p^*)(cv)^2} \tag{6}$$

In the absence of other estimates of ET or EY we may wish to specify θ_j and p to compute EY and ET in the standard manner using (1). As an example of sample sizes needed to estimate p with various levels of precision, we have computed values of K^* using several reasonable combinations of J and p (Table 3). All values in Table 3 were computed using ET and EY under the assumption that

$$\theta_j = \frac{p^{j-1}(1 - p)}{1 - p^J}, \quad j = 1, 2, \ldots, J.$$

Finally, we wish to indicate some uses of the tables for the field biologist. Table 1 shows that when the model assumptions are met and the field biologist uses the approximate confidence interval estimates herein sug-

gested, the actual frequency of coverage is quite close to the theoretical in a wide range of situations. In any one case, however, the estimate of p (and hence also of p^J) can be considerably different from the true value especially when the number of nests in the sample is small (see Max $\hat{p}$ and Min $\hat{p}$ in Table 1). Comparisons of $\hat{p}^J$ and $\bar{Y}$ show that $\hat{p}^J$ is always a better estimate of nesting success when the assumptions of the model obtain, and that the difference in these two estimates is greater in cases of lower overall nesting success.

The precision of the Mayfield estimator in a field situation is of course dependent on how closely the assumptions of the model are met by the population in question. It is doubtful whether this model (or any other probability model of a biological phenomenon for that matter) will reflect exactly the reality of nature. However, the traditional estimator $\bar{Y}$ is almost sure to overestimate nesting success in all situations where nests are found on other than the first day of the nesting period (see for example, Mayfield 1960, 1961, 1975; Custer and Pitelka 1977). If the assumptions of this model approximate the reality of a population, then we suggest its use to correct for the obvious, known bias associated with $\bar{Y}$. In cases where this model seems totally inappropriate we know of no way to accurately estimate nesting success if nests other than first day nests are to be used.

Table 2 gives empirical estimates of the power in testing the null hypothesis that $p_1 = p_2$ against the alternatives that $p_2 = p_1 + \Delta$. This table gives, for selected values of Δ, the probability of rejecting the null hypothesis given that in fact $p_2 = p_1 + \Delta$. Note that for $\Delta \neq 0$ rejecting the null hypothesis is the correct decision, and hence we would hope the probability of rejecting would be large. For $\Delta = 0$ this probability should be the level of significance α for the test. Table 2 shows how the power function varies with changes in Δ, p_1, J, and K. A more detailed discussion of the concept of the power of a statistical test can be found in Cohen (1977).

Table 3 is a guide for the field biologist to determine the number of nests needed in his or her sample in order to achieve a given precision in the estimator. We feel that a sample size of at least 20 nests is needed in all cases (our reasons are given in Table 3) so only calculated sample sizes greater than 20 are presented. As mentioned, the biologist must first make guesses of p, EY and ET or of p and θ_j, j = 1, . . . , J, in order to calculate the sample size required for a specified coefficient of variation using equation (6). Table 3 covers several cases, but direct calculation using (6) is a simple matter in cases not covered in the table.

SUMMARY

Using a nesting model proposed by Mayfield (1960, 1961, 1975) we show that the estimator he proposes is a maximum likelihood estimator (m.l.e.). M.l.e. theory allows us to calculate

the asymptotic distribution of this estimator, and we propose an estimator of the asymptotic variance. Using these estimators we give approximate confidence intervals and tests of significance for daily survival. Monte Carlo simulation results show the performance of our estimators and tests under many sets of conditions. A traditional estimator of nesting success is shown to be quite inferior to the Mayfield estimator. We give sample sizes required for a given accuracy under several sets of conditions.

ACKNOWLEDGMENTS

Jim Hines handled most of the programming associated with the Monte Carlo simulations. Madaline Schumacher and Peggy Bowley typed the manuscript. We wish to thank L. Stokes, F. Percival, P. Geissler, H. Mayfield and A. Dunham for reading the manuscript and providing their comments.

LITERATURE CITED

Cramér, H. 1946. Mathematical methods of statistics. Princeton Univ. Press, Princeton, New Jersey.

Cohen, J. 1977. Statistical power analysis for the behavioral sciences. Academic Press, New York, New York.

Custer, T. W. and F. A. Pitelka. 1977. Demographic features of a Lapland Longspur population near Barrow, Alaska. Auk 94:505–525.

Johnson, D. H. 1979. Estimating nest success: the Mayfield method and an alternative. Auk 96:651–661.

Mayfield, H. 1960. The Kirtland's Warbler. Cranbrook Inst. Sci., Bloomfield Hills, Michigan.

———. 1961. Nesting success calculated from exposure. Wilson Bull. 73:255–261.

———. 1975. Suggestions for calculating nest success. Wilson Bull. 87:456–466.

Miller, H. W. and D. H. Johnson. 1978. Interpreting the results of nesting studies. J. Wildl. Manage. 42:471–476.

PATUXENT WILDLIFE RESEARCH CENTER, LAUREL, MARYLAND 20811 AND MIGRATORY BIRD AND HABITAT RESEARCH LABORATORY, LAUREL, MARYLAND 20811. ACCEPTED 15 DEC. 1979.

Wilson Bull., 93(1), 1981, pp. 54–66

NARROWLY DISJUNCT ALLOPATRY BETWEEN BLACK-CAPPED AND CAROLINA CHICKADEES IN NORTHERN INDIANA

Peter G. Merritt

The Black-capped Chickadee (*Parus atricapillus*) inhabits wooded areas across the northern United States, Canada and high elevations in the southern Appalachian Mountains. This species is replaced geographically by the closely related Carolina Chickadee (*P. carolinensis*) in the mideastern and southern United States (A.O.U. Check-list 1957). Where the ranges adjoin, a variety of situations prevail. In Kansas, the westernmost state where the ranges meet, the southern range of *P. atricapillus* is contiguous with the northern range of *P. carolinensis*. Rising (1968) provided evidence based on multivariate analyses of morphological characters that some interbreeding resulting in hybrid birds may take place there. Following the boundary eastward, the ranges remain contiguous through Missouri and into southern Illinois. There, Brewer (1961, 1963) described a zone of interbreeding where many birds appeared to be hybrids. Eastward from Illinois through Indiana and Ohio, Brewer (1963) reported a narrow gap (about 24 km wide in eastern Illinois) between the breeding ranges. Ward and Ward (1974) reported contiguous ranges in southeastern Pennsylvania and they provided evidence based on song that hybridization may occur there. Johnston (1971) described a hybrid population at the contact zone in the mountains of southwestern Virginia, where the chickadee ranges are separated by elevation. In contrast, Tanner (1952) found an elevational gap of about 180 m (855–1035) between the nesting ranges in the Great Smoky Mountains.

The existence of a narrow gap between the chickadee ranges is peculiar because apparently suitable nesting habitat occurs within the gap regions (Tanner 1952, Brewer 1963). Furthermore, both species appear to be able to exist under essentially the same climatic conditions. In the Great Smoky Mountains where *P. atricapillus* occurs only on some peaks, Tanner (1952) found that *P. carolinensis* nested at higher elevations on the peaks where *P. atricapillus* did not occur. In Illinois, Brewer (1963) found that *P. atricapillus* and *P. carolinensis* occurred along parallel river systems at the same latitude only 32 km apart.

On Mt. LeConte (Great Smoky Mountains), Tanner (1952) observed that *P. atricapillus* dispersed to lower elevations in the winter, invading the range of *P. carolinensis*. As the nesting season approached most *P. atricapillus* withdrew up the slopes resulting in the formation of the gap.

Similar observations are lacking for the latitudinal gap, but the hiatus seems to be most prominent during the breeding season (Brewer 1963). Brewer (1963) suggested that the gap evolved as a reproductive isolating mechanism. Since the hybrid population in Illinois had a relatively low rate of reproductive success (Brewer 1961), selective pressures may have favored an annual movement of chickadees away from the range interface in certain regions; this would act to increase the fitness of these birds. This hypothesis can be falsified by demonstrating that the gap does not form prior to reproduction.

This paper describes a field study examining the range relationship of *P. atricapillus* and *P. carolinensis* in northern Indiana. The study was designed to test the prediction that after a dispersal of either species of chickadee towards the range interface during the winter, these individuals withdraw from that region, forming a gap between the ranges before reproduction takes place.

STUDY AREA AND METHODS

Fieldwork was conducted in Kosciusko, Wabash and adjacent counties in Indiana. Drainage for most of the study area is by way of the Wabash River system which empties south into the Ohio River. The northern part of the study area consists of gently rolling hills characteristic of glacial landforms; the southern part is a flat till plain. Around 1820, beech-maple (*Fagus-Acer*) and oak-hickory (*Quercus-Carya*) forests were the dominant vegetation types in the study area (Lindsey et al. 1965). Today most of the land is farmed, the main crops being corn, wheat and soybeans. Wooded areas occur along river systems or as isolated woodlots. Lindsey (1966) gives additional information on climate and other aspects of natural history of the area.

Preliminary fieldwork indicated that *P. atricapillus* occurred near the city of Warsaw, Kosciusko Co., and *P. carolinensis* occurred along the Wabash River in Wabash County. Six relatively undisturbed stands of mesic forest were chosen as trapping stations along a 72 km north-south line transecting this region (Merritt 1977). Feeders erected at each trapping station were filled with sunflower seeds when originally set up, and a constant supply of seed was maintained until May 1976. Trapping was conducted with 6 McCamey chickadee traps (McCamey 1961) on at least 4 separate days totaling about 25 h at each station, from 24 December 1975–4 April 1976. Captured chickadees were held briefly for banding, measurement and observation of plumage coloration. The birds were marked with U.S. Fish and Wildlife Service aluminum bands and from 1–3 plastic color leg bands for individual recognition.

Captured chickadees were identified on the basis of tail-to-wing ratio and feather coloration. Wing chord and tail measurements were taken as suggested by Baldwin et al. (1931, see Merritt 1978). Inspection of plumage color was limited to the outer edge of the lateral tail feathers and the lateral edges of the secondary wing feathers. These areas are characteristically distinct and white in *P. atricapillus*, but are gray and less distinct in *P. carolinensis*. Notes were taken on the coloration of these feathers as compared with a color chart consisting of 5 gradations ranging from white to gray. The chart was constructed by reference to feathers of specimens of *P. atricapillus*, *P. carolinensis* and suspected hybrids from Illinois.

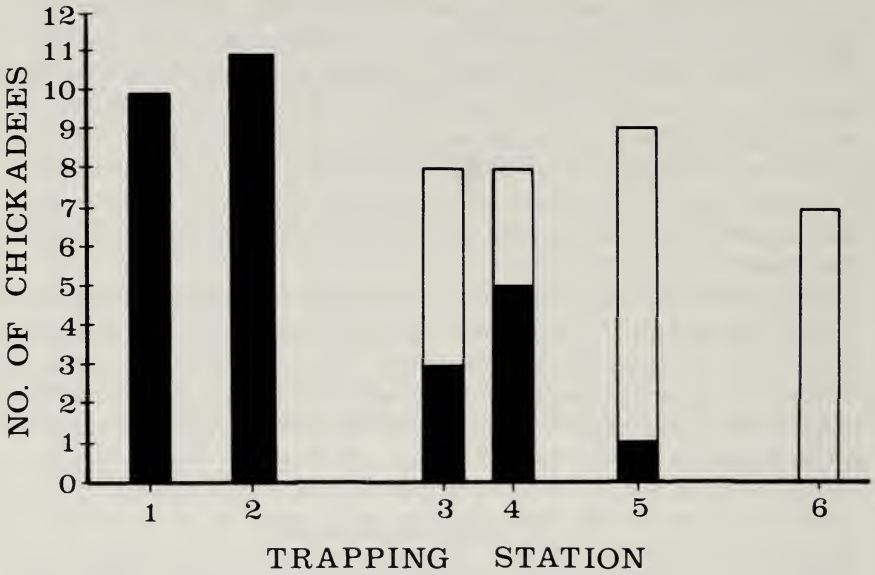


FIG. 1. The number of chickadees banded at each trapping station; *P. atricapillus* is shown in solid bars and *P. carolinensis* in open bars. The relative north-south distance between stations is represented on the abscissa.

Other distributional information was gained by soliciting vocal responses from chickadees in non-trapping areas in the winter (27 January–26 February 1976) and spring (29 April–31 May 1976). *P. atricapillus* typically sings a 2-noted whistle song, *fee-bee*, which is generally distinct from the 4-noted song, *fee-bee-febay*, of *P. carolinensis*. Less distinct, yet diagnostic to each species (especially when an on-the-spot comparison with a pre-recorded tape can be made), is the general call note. *P. atricapillus* gives this as a relatively slow *chickadee-dee-dee*, whereas *P. carolinensis* gives the same call but faster.

A portable cassette tape recorder was used to broadcast pre-recorded chickadee songs. One min of song and call notes for each species was recorded on separate cassettes. Songs of both species and call notes for *P. atricapillus* were recorded from Kellogg and Allen (1971) and call notes for *P. carolinensis* were recorded from Borror (1970). I located wooded areas containing seemingly favorable habitat for chickadees. Up to 30 min were spent walking through each area trying to elicit song responses from chickadees. This was accomplished by continuously broadcasting the pre-recorded tapes (once a minute I would pause to rewind the tape and listen for chickadees). During the winter survey I broadcast the *atricapillus* tape at areas north of the Eel River, the *carolinensis* tape at areas south of the Wabash River and both tapes, interchanging them at 5-min intervals, between the Eel and Wabash rivers. Because of changes in the chickadee populations found at the trapping stations this procedure was modified for the spring survey. The *atricapillus* tape was broadcast at areas north of the Eel River, the *carolinensis* tape at areas south of the Eel River and both tapes at areas along the Eel River. The trapping stations were also included in the spring survey.

Approximately 10 h of observation on 4 separate visits were spent at each of the 6 trapping stations from 6 April–22 May 1976. An additional 3 h of observation were spent at trapping

stations 5 and 6 on 25 May. The observation time was spent searching for and following chickadees.

TRAPPING RESULTS

The winter ranges of the 2 species were found to overlap by at least 20 km (Fig. 1). Thirty individuals of *P. atricapillus* were banded at trapping stations 1–5 and 23 individuals of *P. carolinensis* were banded at stations 3–6. Characteristics of the captured chickadees are described and compared in a separate paper (Merritt 1978); only features necessary for species identification are included in the following discussion.

The tail-to-wing ratio ranged from 0.846–0.938 ($\bar{x}$ = 0.890, SD = ±0.023) in *P. carolinensis* and 0.919–0.992 ($\bar{x}$ = 0.955, SD = ±0.016) in *P. atricapillus*. The overlap in tail-to-wing ratio (9.4% of all chickadees captured) is not uncommon; Lunk (1952), Tanner (1952), Simon (1959), Brewer (1963) and Johnston (1971) have reported slight overlap in the tail-to-wing ratio of these species.

Accurate classification of plumage color was difficult in the field because lighting conditions varied, but some differences in coloration were evident. Four *P. atricapillus* (13.3%) and 4 *P. carolinensis* (17.4%) showed plumage coloration tending towards intermediacy. These percentages of individuals deviating from the characteristic forms are within the range of variation observed by Brewer (1963:16–17) in Illinois.

One *P. atricapillus* banded at station 2 and 1 *P. carolinensis* banded at station 5 were intermediate in tail-to-wing ratio and feather coloration. Their intermediate morphology may have resulted from interbreeding; however, it is not likely that hybridization is widespread within the study area since these individuals represent only 3.8% of all chickadees captured.

WINTER DISTRIBUTION

The winter survey of vocal responses indicated that the ranges of *P. atricapillus* and *P. carolinensis* overlapped by about 25 km (Fig. 2). Differences in time and day of sampling did not seem to affect this survey significantly; chickadees responded with call notes or song at all 58 areas sampled. The distributional map in Fig. 2 may be biased to some extent by the choice of songs broadcast at a particular area. However, this bias is probably minimal since on several occasions an individual of 1 species responded to the taped broadcast of the heterospecific song (Merritt 1978) and the amount of range overlap detected (Fig. 2) corresponds with that found by the trapping (Fig. 1).

Typical vocal responses were elicited at most areas permitting species identification, but at 1 location an individual chickadee gave the song of

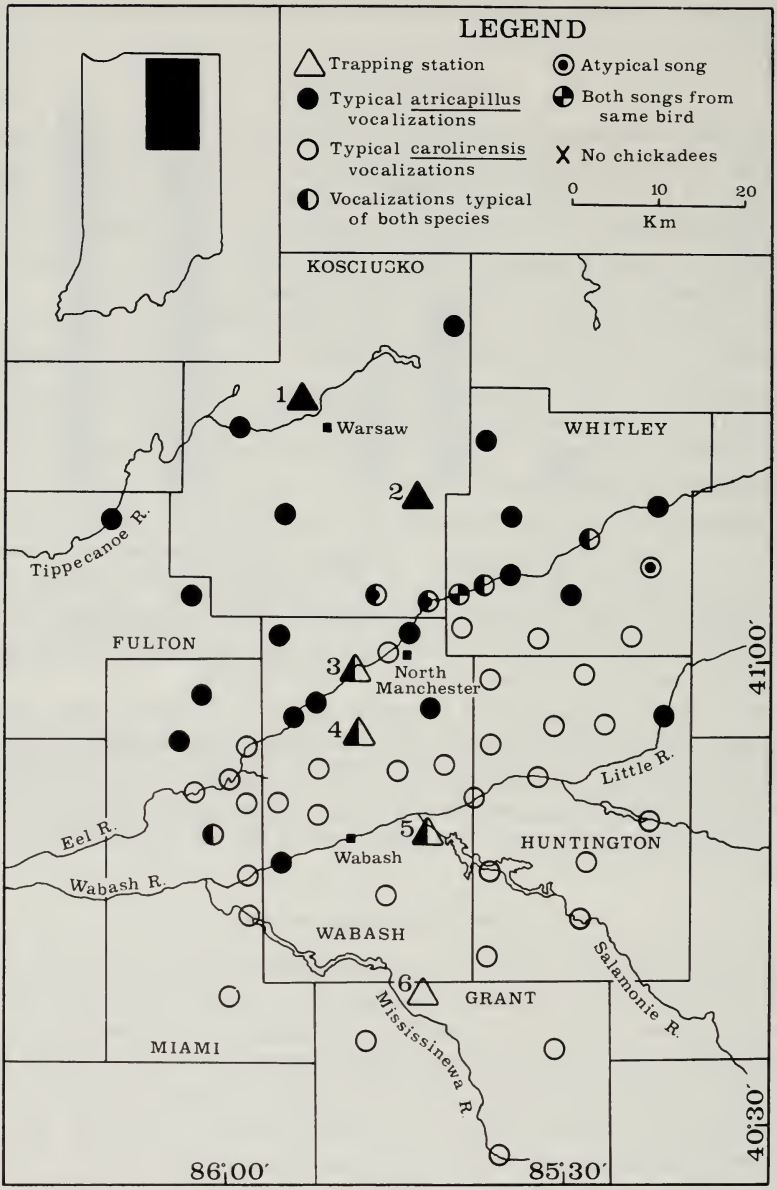


FIG. 2. Winter distribution of chickadees as determined by vocal responses. The trapping station symbols are solid if *P. atricapillus* was present, open if *P. carolinensis* was present and half-filled-in if both species were present.

both species and at 3 other locations abnormal songs were elicited (Merritt 1978). Tanner (1952), Johnston (1971) and Ward and Ward (1974) also observed individual chickadees singing the songs of both species. Similar cases of closely related species singing mixed songs have been described in buntings (*Passerina cyanea* and *P. amoena*), meadowlarks (*Sturnella neglecta* and *S. magna*), towhees (*Pipilo fuscus* and *P. albicollis*), treecreepers (*Certhia familiaris* and *C. brachydactyla*), Old World warblers (*Acrocephalus scirpaceus* and *A. palustris*, *Phylloscopus trochilus* and *P. collybita*, *Sylvia communis* and *S. atricapilla*) and wrens (*Troglodytes aedon* and *Thryomanes bewickii*) (Lemaire 1977:227–230). As suggested by Emlen et al. (1975) for the case of the buntings (*Passerina cyanea* and *P. amoena*), it is likely that this behavior promotes interspecific recognition and facilitates heterospecific spacing.

The atypical songs given by 2 chickadees consisted of 4 high-pitched whistle notes of equal tone. The other atypical song consisted of a trill followed by 3 high-pitched whistle notes. In each case, these songs seemed to be given with unusually high intensity. Vocal anomalies apparently similar to these were also reported in Illinois (Brewer 1961, 1963), Kansas (Rising 1968), southwestern Virginia (Johnston 1971) and southeastern Pennsylvania (Ward and Ward 1974). Brewer (1963) and Johnston (1971) noted an unusually high percentage of atypical vocalizations near the hybrid zones in Illinois and Virginia, respectively. It seems probable that the vocal anomalies are the result of interbreeding. In this study only 3 individuals in the 58 areas surveyed responded with abnormal songs. This suggests, as does the trapping data, that isolated cases of interbreeding may occur in northern Indiana but a significant zone of hybridization is not present.

SPRING DISTRIBUTION

The spring survey of vocal responses revealed that the ranges of *P. atricapillus* and *P. carolinensis* were separated by a gap of about 30 km (Fig. 3). In general, chickadees of both species were sparse throughout the region surveyed; rarely did more than 1 chickadee in any particular area respond to the taped broadcast. Most chickadees occurred in river bottom forests or lowland woods along streams. This was especially true for *P. atricapillus*; only twice were individuals located in isolated woodlots.

Only 1 *P. atricapillus* was found south of the Tippecanoe River and only 1 *P. carolinensis* was found north of the Eel River. Perhaps the most striking feature of the gap was the absence of chickadees along the Eel River northeast of trapping station 3. This area offers habitat similar to that existing along the Elkhart, Tippecanoe and Wabash rivers, yet in

spite of repeated tries at various times on different days no chickadees could be found here.

TRAPPING STATION OBSERVATIONS

Of the 30 banded individuals of *P. atricapillus*, only 9 were seen past the middle of March and only 2 were observed after 1 April (Fig. 4). One of these (at station 2) was seen on both 8 and 15 April accompanied by an unbanded individual. Of the 23 banded individuals of *P. carolinensis*, 16 were observed in April and 4 individuals (at stations 4, 5 and 6) were seen near the end of May. During the observations at stations 5 and 6, typical *carolinensis* songs were commonly heard and a few instances of what appeared to be territorial combat were observed.

The only other sightings of chickadees at any of the trapping stations during April and May were as follows: On 3 April, I followed 3 unbanded chickadees from 16:00–16:10 as they foraged from the center of station 2 to the north edge of the woods. At least one of the birds gave the 2-noted whistle song characteristic of *P. atricapillus* several times, but the song was given softly. When they reached the edge of the woods they hesitated for a minute, then flew north over a corn field out of sight. On 13 April and 16 May, I observed an unbanded chickadee foraging in woods along the Eel River about 0.4 km north of station 3; no vocalizations were heard. On 25 May, I saw a group of 4 chickadees as they foraged slowly through some dense vegetation at station 6. One bird wore a band and appeared to be a parent leading young.

DISCUSSION

Comparison of the spring distribution (Fig. 3) with the winter distribution (Fig. 2) makes it evident that most *P. atricapillus* withdrew from the range interface. Observations at the trapping stations indicate that this took place primarily during the last 2 weeks of March (Fig. 4). The withdrawal included *P. atricapillus* occupying woodlots in Elkhart County as far as 80 km north of the range interface. Interestingly, most of the chickadees found in this region were in riparian habitat. In Kalamazoo County, Michigan, 175 km north of the range interface, *P. atricapillus* is common in woodlots as well as riparian habitat at all times of the year (pers. obs.). It seems likely that in northern Indiana chickadees were found mainly in riparian habitat because the only continuous stretches of woodland habitat occur along the river systems and these areas act as avenues of dispersion for the southernmost breeding *P. atricapillus*.

Seasonal migration in *P. atricapillus* has been discussed by Butts (1931), Wallace (1941), Bent (1946) and Lawrence (1958). Examination of unpublished banding records obtained in December 1978 from the U.S.

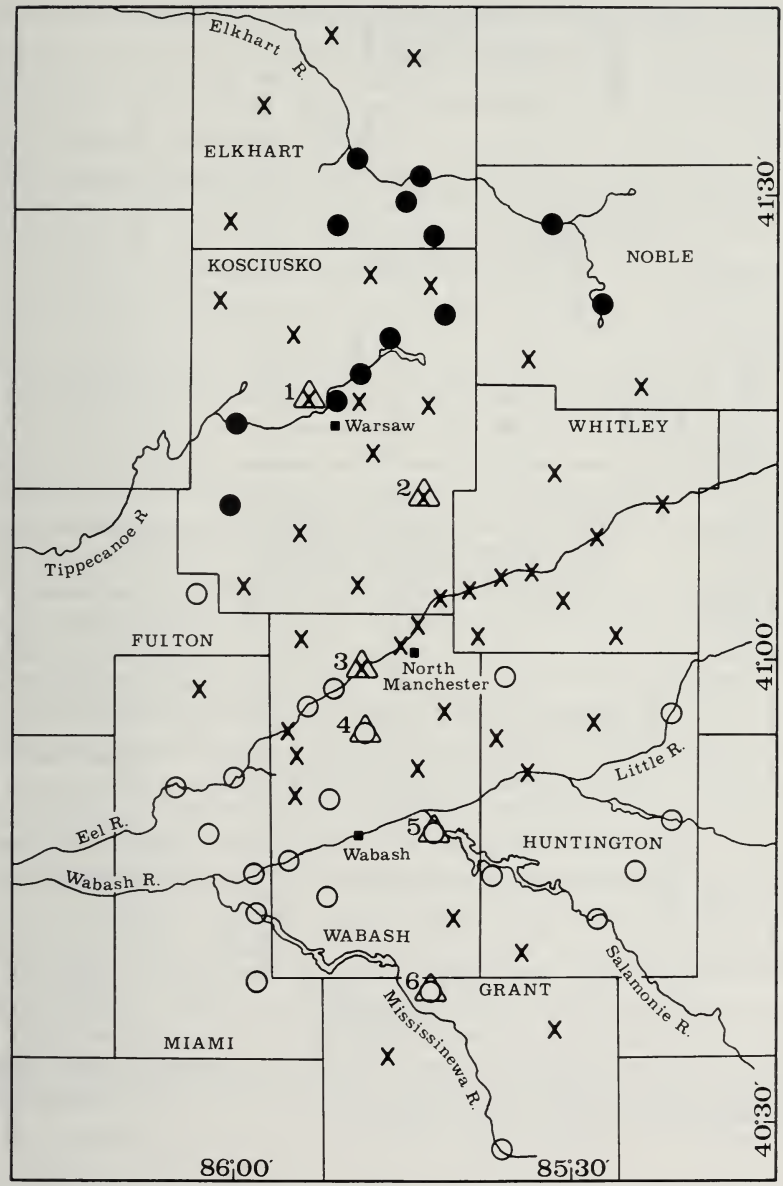


FIG. 3. Spring distribution of *P. atricapillus* and *P. carolinensis*. (Refer to legend in Fig. 2.)

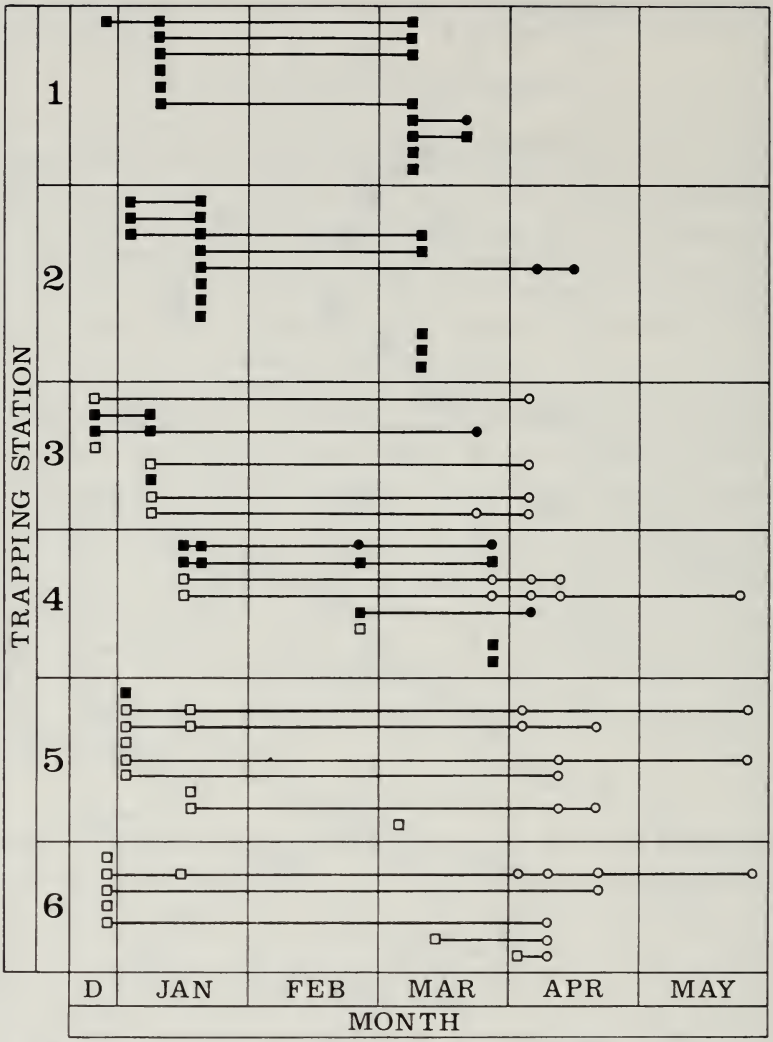


FIG. 4. Summary of captures and observations at the trapping stations. Squares indicate the bird was captured and circles indicate it was observed. *P. atricapillus* is represented by solid symbols and *P. carolinensis* by open symbols.

Fish and Wildlife Service indicates that long distance movements of *P. atricapillus* are most common in a northeast-southwest direction throughout the eastern and midwestern U.S. and southeastern Canada. Since numerous banding studies show that many individuals of *P. atricapillus* are permanent residents in this region (e.g., Odum 1942, Glase 1973,

Weise and Meyer 1979), it appears that during the winter the gap between the ranges may become occupied by individuals of *P. atricapillus* from the northeast. The gap becomes apparent only after the withdrawal of *P. atricapillus* in the spring. Observations in Ohio by Thomas (1958) also agree with this conclusion.

The disjunct nature of the breeding ranges of *P. atricapillus* and *P. carolinensis* appears to be relatively stable; the gap has remained at approximately the same latitude in northern Indiana for at least 40 years. From 1935–1939 Ernest M. Shull frequently went on early morning walks from Manchester College along the Eel River, upstream about 3.2 km to the town of Liberty Mills and then back. This area lies only a few kilometers northeast of trapping station 3. Shull (unpubl.) recorded sightings of all birds along this route. Downy Woodpeckers (*Picoides pubescens*), Tufted Titmice (*P. bicolor*) and White-breasted Nuthatches (*Sitta carolinensis*) were common during every month of the year. Chickadees (most reported to be *P. atricapillus*), however, were found in January through April and September through December, but none in May or July and only 1 in each of June and August during these years.

It is still not clear what factors cause the gap to occur. The fact that the elevational gap found by Tanner (1952) in the Great Smoky Mountains and the latitudinal gap found in northern Indiana both occurred only during the breeding season and became obvious after a withdrawal of *P. atricapillus* suggests that similar factors maintain the gap at both locales. Considering ultimate factors, Brewer (1963) suggested that the gap evolved as a reproductive isolating mechanism functioning to reduce unsuccessful interbreeding. No active chickadee nests were found in this study so to test Brewer's reproductive isolation hypothesis it is necessary to estimate the time of reproduction. The expected date of first egg-laying by chickadees at the range interface in northern Indiana can be approximated by adjusting data for chickadees nesting in Illinois. Both species tend to begin laying about 3.5–4.5 days later for each degree of latitude northward (Brewer 1961), so the first egg-laying at 41°N latitude should occur from 20 April–26 May for *P. atricapillus* and 30 April–21 May for *P. carolinensis*. Nest-building, excavation and the establishment of territorial boundaries precede the first egg-laying by about 20 days. Therefore, chickadees remaining in the study area might engage in reproductive activities as early as 1 April for *P. atricapillus* and 10 April for *P. carolinensis*. The main withdrawal of chickadees away from the range interface took place prior to these dates so the prediction that the gap forms before nesting activities begin is supported. This, plus the fact that only a few possible hybrid individuals were found in this study, indicate that the gap functions as a reproductive isolating mechanism, but it is not clear that the gap

evolved for this purpose. If an individual chickadee's fitness can be increased by migrating to another area to breed, then natural selection may have favored the spring withdrawal of *P. atricapillus* from the range interface; however, this hypothesis remains speculative.

Two other hypotheses attempting to explain narrowly disjunct allopatry in general, and thought possibly to apply to the case of the chickadees, rely chiefly on proximate factors. Cornell (1974) suggested that parasites might be transmitted between chickadee species in the overlap zone. If these had an adverse effect on the reproductive success of chickadees breeding at the range interface a gap could develop. Expanding on MacArthur's (1972) model of exploitative competition, Slade and Robertson (1977) suggested that a change in resource availability as a result of the cost of interspecific competition in the overlap zone may have caused a competitively-induced gap. These hypotheses do not assume that the withdrawal of *P. atricapillus* is related to the maintenance of the gap. They both require that interspecific contact occurs between chickadees that are permanent residents at the range interface. If the interactions severely reduce the fitness of chickadees attempting to breed in this region a gap might develop. For an hypothesis of this type 2 predictions can be made: (1) the width of the gap should be dependent upon the degree of overlap exhibited by sedentary individuals of both species; and (2) the width of the gap should fluctuate in time according to the rate of recolonization. A gap developing under these circumstances might persist for a relatively long period of time if the rate of recolonization is low. Therefore, these hypotheses might only be testable by a long term study monitoring the distribution and abundance of permanent residents at the range interface.

It is also possible that the gap is caused and maintained by the winter influx of *P. atricapillus*. These individuals might provide additional competition for limiting food resources, which may result in decreasing the winter survival rate of resident chickadees of both species at the range interface. This might be especially important in forming the gap if hybrid chickadees are inferior competitors. This hypothesis could be examined by testing the prediction that year-to-year fluctuations in sedentary chickadee populations near the range interface are directly related to the intensity of the winter influx of *P. atricapillus*.

SUMMARY

During the winter and early spring of 1975–1976 the ranges of *Parus atricapillus* and *P. carolinensis* overlapped by about 25 km in northern Indiana. Evidence based on morphology and song suggest that isolated cases of interbreeding may occur. During the last 2 weeks of March most *P. atricapillus* withdrew from the range interface. A survey of vocal responses

conducted from 29 April–31 May revealed that the breeding ranges were separated by a gap of about 30 km. The withdrawal of *P. atricapillus* included individuals occupying woodlots as far as 80 km north of the range interface.

It is still not clear what factors cause the gap to occur. The resemblance of the elevational gap found by Tanner (1952) in the Great Smoky Mountains and the latitudinal gap found in northern Indiana suggests that the gap is maintained by similar factors at both locations. Since the gap becomes obvious with the withdrawal of *P. atricapillus* just prior to the breeding season, it is possible that these movements were selected for as a reproductive isolating mechanism.

Other hypotheses attempting to explain the presence of the gap rely chiefly on proximate factors. The most likely of these hypotheses are: (1) the gap forms as a direct result of interspecific interactions between sedentary chickadees at the range interface; and (2) the gap is caused and maintained by the winter movement of *P. atricapillus* to the range interface. Competitive interactions reducing the fitness of sedentary chickadees in and near the gap may be important for either hypothesis.

ACKNOWLEDGMENTS

I am grateful to Richard Brewer for providing guidance throughout all phases of this project. Richard F. Johnston, Julian C. Lee, Oscar T. Owre, James D. Rising and Edwin O. Willis read drafts of this manuscript and provided useful suggestions. James Bostwick, Neil Case, James B. Cope, David Eiler, Russell E. Mumford, Ernest M. Shull, Paul Steffen and Rex Watters contributed useful information. Doug and Christine Campbell, John Olson and John Stiner helped with the fieldwork. This project was completed in partial fulfillment of the Master of Arts Degree at Western Michigan University, Kalamazoo, Michigan. Funding was provided by grants from the Frank M. Chapman Memorial Fund of the American Museum of Natural History and the Western Michigan University Research Fund.

LITERATURE CITED

American Ornithologists' Union Check-list Committee. 1957. Check-list of North American birds, 5th ed. Lord Baltimore Press, Baltimore, Maryland.

Baldwin, S. P., H. C. Oberholser and L. G. Worley. 1931. Measurements of birds. Sci. Publ. Cleveland Mus. Nat. Hist. 2.

Bent, A. C. 1946. Life histories of North American jays, crows, and titmice. U.S. Natl. Mus. Bull. 191.

Borror, D. J. 1970. Common bird songs (sound recording). Dover Publ., Inc., New York, New York.

Brewer, R. 1961. Comparative notes on the life history of the Carolina Chickadee. Wilson Bull. 73:348–373.

———. 1963. Ecological and reproductive relationships of Black-capped and Carolina chickadees. Auk 80:9–47.

Butts, W. K. 1931. A study of the chickadee and White-breasted Nuthatch by means of marked individuals. Pt. II: the chickadee (*Penthestes atricapillus atricapillus*). Bird-Banding 2:1–26.

Cornell, H. 1974. Parasitism and distributional gaps between allopatric species. Am. Nat. 108:880–883.

Emlen, S. T., J. D. Rising and W. L. Thompson. 1975. A behavioral and morphological study of sympatry in the Indigo and Lazuli buntings of the Great Plains. Wilson Bull. 87:145–179.

Glase, J. C. 1973. Ecology and social organization in the Black-capped Chickadee. Living Bird 12:235–267.

Johnston, D. W. 1971. Ecological aspects of hybridizing chickadees (*Parus*) in Virginia. Am. Midl. Nat. 85:124–134.

Kellogg, P. P. and A. A. Allen. 1971. A field guide to bird songs of eastern and central North America (sound recording). Houghton Mifflin Co., Boston, Massachusetts.

Lawrence, L. de K. 1958. On regional movements and body weight of Black-capped Chickadees in winter. Auk 75:415–443.

Lemaire, F. 1977. Mixed song, interspecific competition and hybridization in the Reed and Marsh warblers (*Acrocephalus scirpaceus* and *palustris*). Behaviour 63:215–240.

Lindsey, A. A. (ed.) 1966. Natural features of Indiana. Indiana Acad. Sci., Indianapolis, Indiana.

———, W. B. Crankshaw and S. A. Qadir. 1965. Soil relations and distribution map of the vegetation of presettlement Indiana. Botan. Gaz. 126:155–163.

Lunk, W. A. 1952. Notes on variation in the Carolina Chickadee. Wilson Bull. 64:7–21.

MacArthur, R. H. 1972. Geographical ecology: patterns in the distribution of species. Harper and Row, Publishers, Inc., New York, New York.

McCamey, F. 1961. The chickadee trap. Bird-Banding 32:51–55.

Merritt, P. G. 1977. Gap formation: a reproductive isolating mechanism for *Parus atricapillus* and *P. carolinensis* in northern Indiana. M. A. thesis, Western Michigan Univ., Kalamazoo, Michigan.

———. 1978. Characteristics of Black-capped and Carolina chickadees at the range interface in northern Indiana. Jack-Pine Warbler 56:171–179.

Odum, E. P. 1942. Annual cycle of the Black-capped Chickadee—3. Auk 59:499–531.

Rising, J. D. 1968. A multivariate assessment of interbreeding between the chickadees, *Parus atricapillus* and *P. carolinensis*. Syst. Zool. 17:160–169.

Simon, S. W. 1959. Occurrence and measurements of Black-capped Chickadees at Monkton. Md. Maryland Birdlife 15:3–4.

Slade, N. A. and P. B. Robertson. 1977. Comments on competitively-induced disjunct allopatry. Occ. Pap. Mus. Nat. Hist., No. 65, Univ. Kansas, Lawrence, Kansas.

Tanner, J. T. 1952. Black-capped and Carolina chickadees in the southern Appalachian Mountains. Auk 69:407–424.

Thomas, E. S. 1958. The Black-capped Chickadee in central Ohio. Wheaton Club Bull. 3 (new ser.):8–11.

Wallace, G. J. 1941. Winter studies of color-banded chickadees. Bird-Banding 12:49–67.

Ward, R. and D. A. Ward. 1974. Songs in contiguous populations of Black-capped and Carolina chickadees in Pennsylvania. Wilson Bull. 86:344–356.

Weise, C. M. and J. R. Meyer. 1979. Juvenile dispersal and development of site-fidelity in the Black-capped Chickadee. Auk 96:40–55.

DEPT. BIOLOGY, UNIV. MIAMI, CORAL GABLES, FLORIDA 33124. ACCEPTED 1 DEC. 1979.

Wilson Bull., 93(1), 1981, pp. 67–76

TOE FUSION IN OSCINES

George A. Clark, Jr.

Although striking differences in extent of webbing between the toes of nonpasserines are well-known and often used to illustrate adaptation in birds, the degree of connection between the toes in oscines has received much less attention. Ridgway (1901–07) in scattered keys and descriptions commented on integumental fusion of the toes of numerous New World oscine taxa, but provided little interpretation on possible significance of the taxonomic variations, apart from their use in distinguishing taxa. Although others (e.g., Rand and Traylor 1953) have occasionally commented on fusion in oscines, a comprehensive survey of the families is lacking. I attempt here to interpret major taxonomic differences in fusion in relation to systematics and behavioral differences and to indicate problems for future study.

MATERIALS AND METHODS

I examined study skins of 1941 species of oscines in the collections of the National Museum of Natural History (Washington, D.C.), American Museum of Natural History (New York), British Museum (Nat. Hist., Tring) and the University of Connecticut. In addition, I made more than 175 observations of toe positions in perching or standing for wild or captive birds representing 30 species. The taxonomic sequence follows Morony, Bock and Farrand (1975).

To examine fusion among the 3 forward toes I used a hand lens or binocular dissecting microscope, except for species of large size. Degree of fusion of the middle (III) and outer (IV) toes is primarily emphasized, but extent of fusion of the inner (II) and middle toes was noted for 349 species, as discussed below. I selected as a major landmark for comparison the articulation between the first and second phalanges of the middle toe, located by bends in that toe, by the plantar flexion creases and, in many cases, by an overlying scute termed the proximal cap (Clark 1977). Fusion of toes III and IV is rated low (L) if not reaching distally to the region of articulation between the first and second phalanges of III, moderate (M) if reaching that region, and high (H) if extending further distally (Fig. 1). These ratings are arbitrary divisions of a continuum, but the extremes of low vs high fusion are markedly different. This summary of fusion in 3 categories provides less detail than sometimes given by Ridgway (1901–07), but is advantageous in facilitating comparisons across a wide range of taxa.

RESULTS AND INTERPRETATION

In tabulating data on fusion of toes III and IV (Table 1), I emphasize particularly the distribution of extreme differences (low vs high) and the condition in many genera considered atypical in their assigned families. Such a summarizing list (Table 1) necessarily obscures many finer taxonomic differences. For example, nearly all genera of the Mimidae have

FIG. 1. Examples of toe fusion, from left to right: low, House Sparrow (*Passer domesticus*); moderate, White-breasted Nuthatch (*Sitta carolinensis*); and high, Red-eyed Vireo (*Vireo olivaceus*). The arrows mark the approximate level of the joint between phalanges 1 and 2 of the middle toe.

low fusion, but the inclusion of *Donacobius* extends the mimid range to the moderate level.

Partial associations exist between degree of fusion and behavior. The terrestrial larks (Alaudidae) and pipits (Motacillidae) have low to moderate fusion, whereas many predominantly arboreal Old World families have moderate to high fusion, e.g., Campephagidae, Irenidae, Dicaeidae, Nectariniidae, Zosteropidae, Meliphagidae, Oriolidae, Dicruridae. Families that climb on tree trunks or other vertical surfaces often have moderate to high fusion, e.g., Sittidae, Certhiidae, Climacteridae. Still other Old World families or subfamilies range from low to high fusion, e.g., Laniidae, Timaliinae, Sylviinae, Malurinae. Finches, sparrows and buntings throughout the world (Emberizinae, Cardinalinae, Carduelinae, Estrildidae, Ploceidae) have low to moderate fusion, a level widespread in the New World 9-primaried assemblage, including Parulidae, Drepanididae and Icteridae. However, vireos (Vireonidae), including peppershrikes (*Cyclarhis*) and shrike-vireos (*Vireolanius*), have greater fusion.

Species within a genus are usually similar in the broad categories of toe fusion used here (Table 1), but a few Old World genera, the warblers *Cettia* and *Bradypterus* and the bush-shrikes *Telophorus*, exhibit exceptional interspecific differences. Within *Cettia*, for example, the low fusion of *C. squameiceps*, *C. major* and *C. brunnifrons* contrasts with high fusion of *C. fortipes*; other species are intermediate. Among the 10 examined species of *Bradypterus*, only *B. seebohmi* has high fusion, the other 9 being low. *Telophorus bocagei*, *T. sulfureopectus*, *T. olivaceus*, *T. nigrifrons* and *T. multicolor* have high fusion in contrast to low to moderate in *T. zeylonus*, *T. viridis*, *T. quadricolor* and *T. dohertyi*. In *Telophorus*, separation of groups of species by degree of fusion matches taxonomic units recognized on other characters (Hall and Moreau 1970), but fusion differences within *Cettia* and *Bradypterus* do not parallel taxonomic

Table 1

Fusion of Toes III and IV in Oscines

Taxa	No. species examined	Fusion[a]
Alaudidae	39	L-M
Hirundinidae	43	L-M
plus		
Atticora	2	H
Neochelidon	1	H
Motacillidae	47	L
Campephagidae	53	M-H
plus		
Chlamydochaera	1	L
Pycnonotidae	12	M-H
plus		
Spizixos	1	L
Hypsipetes	1	L
Irenidae	4	M-H
Laniidae		
Prionopinae	7	M-H
Malaconotinae	24	M-H
plus		
Telophorus	9	L-H
Laniinae	22	L-M
Pityriasinae	1	H
Vangidae	9	H
plus		
Hypositta	1	H
Bombycillidae	6	L
plus		
Phainoptila	1	M
Dulidae	1	M
Cinclidae	5	L
Troglodytidae	20	L-M
Mimidae	12	L-M
Prunellidae	8	L
Muscicapidae		
Turdinae	261	L-M
Orthonychinae		
Orthonyx	2	H
Androphobus	1	H
Psophodes	1	M
Sphenostoma	1	M
Cinclosoma	1	L
Eupetes	1	M
Melampitta	1	L
Ifrita	1	H

TABLE 1
CONTINUED

Taxa	No. species examined	Fusion[a]
Timaliinae	38	L-M
plus		
Garritornis	1	H
Stachyris	10	M-H
Rhopocichla	1	H
Macronus	4	M-H
Micromacronus	1	H
Timalia	1	H
Pteruthius	4	M-H
Alcippe	7	M-H
Yuhina	3	M-H
Panurinae	7	L-M
Picathartinae	1	L
Polioptilinae		
Microbates	1	H
Ramphocaenus	1	H
Polioptila	2	M
Sylviinae	128	L-M
plus		
Psamathia	1	H
Cettia	9	L-H
Bradypterus	10	L-H
Acrocephalus	21	M-H
Hippolais	3	M-H
Bathmocercus	1	H
Macrosphenus	1	H
Malurinae		
Malurini	12	M-H
plus		
Amytornis	2	L
Stipiturus	1	L
Acanthizini	26	L-M
plus		
Gerygone	5	M-H
Mohouini	3	M-H
Epthianurini	4	L-M
Genus *incertae sedis*		
Lamprolia	1	M
Muscicapinae		
Bradornis	2	L-M
Melaenornis	3	L-M
Fraseria	1	M
Rhinomyias	2	L-M
Ficedula	15	L-M
Niltava	12	L-M

TABLE 1
CONTINUED

Taxa	No. species examined	Fusion[a]
Muscicapa	14	L-M
Myioparus	2	L-M
Humblotia	1	M
Newtonia	2	M-H
Microeca	4	M-H
Peltops	2	M-H
Petroica	5	L-M
Tregellasia	3	M
Eopsaltria	2	M
Philentoma	1	H
Poecilodryas	4	M-H
Peneothello	1	M
Pachycephalopsis	1	H
Platysteirinae	16	M-H
Monarchinae	54	M-H
Rhipidurinae	22	M-H
Pachycephalinae	34	M-H
plus		
Hylocitrea	1	L
Genus *incertae sedis*		
Turnagra	1	M
Aegithalidae	7	M-H
Remizidae	7	M-H
Paridae	33	M
Sittidae	22	M-H
Certhiidae	6	M-H
Rhabdornithidae	2	M
Climacteridae	5	H
Dicaeidae	48	M-H
Nectariniidae	94	M-H
Zosteropidae	47	M-H
Meliphagidae	110	M-H
Emberizidae		
Emberizinae	42	L-M
Catamblyrhynchinae	1	M
Cardinalinae	8	L
Thraupinae	24	L-M
Tersininae	1	L
Parulidae	41	L
plus		
Zeledonia	1	L
Drepanididae	11	L-M
Vireonidae	38	M-H
Icteridae	19	L-M

Table 1
Continued

Taxa	No. species examined	Fusion[a]
Fringillidae		
Fringillinae	1	L
Carduelinae	17	L-M
Estrildidae	9	L-M
Genus *incertae sedis*		
Pholidornis	1	M
Ploceidae	15	L-M
Sturnidae	14	L
plus		
Buphagus	1	M
Oriolidae	22	M-H
Dicruridae	17	M-H
Callaeidae	3	L
Grallinidae	4	M
Artamidae	9	M-H
Cracticidae	7	M-H
Ptilonorhynchidae	11	L-H
Paradisaeidae	31	M-H
Corvidae	93	L-M
plus		
Platylophus	1	H
Crypsirina	2	M-H
Temnurus	1	H

[a] Symbols: L = low, M = moderate, H = high.

groups of species. Unfortunately, little has been reported about the use of the feet in *Cettia*, *Bradypterus* and *Telophorus*; species of the first 2 are widely noted as difficult to observe as they skulk in brush.

Fusion of toes II and III.—Fusion of toes II and III extends less far distally than that between III and IV. The relatively few taxa with fusion of II and III reaching distally to the vicinity of the articulation of phalanges 1 and 2 of toe III also have high fusion of toes III and IV, e.g., Vangidae, *Orthonyx*, *Microbates*, *Ramphocaenus*, certain muscicapid flycatchers, *Hypositta*, *Certhia*, *Climacteris*, Vireonidae.

Evolution and systematics.—The taxonomic distribution of different degrees of fusion including variation within genera, subfamilies and families shows that evolutionary convergence has been frequent. Among birds as a whole, and among oscines, high fusion between toes is probably usually a derived, rather than primitive, condition. However, reduction of high

fusion remains a hypothetical possibility and might have occurred occasionally. Raikow (1978) suggested that in situations where evolutionarily primitive and derived conditions are indeterminable, systematists should use characters phenetically while recognizing that resulting hypotheses on relationships will be relatively weak. Any systematic suggestions for oscines based heavily on similarity of toe fusion would be at best tentative, but where fusion agrees with other characters in differing markedly between genera traditionally hypothesized to be closely related, reconsideration of affinities seems warranted, as in certain of the following examples.

The monotypic *Chlamydochaera* from Borneo is the sole genus of the cuckoo-shrikes (Campephagidae) with low fusion. Ames (1975) found that *Chlamydochaera* was unique among examined campephagids in having a thrush-like syrinx and concluded that the genus belongs in the thrushes (Turdidae). The low fusion of the toes is also like that of thrushes. In addition, Ames found thrush-like syringes in the muscicapine genera *Bradornis*, *Melaenornis*, *Rhinomyias*, *Ficedula*, *Niltava* and *Muscicapa*, which, unlike most other Old World flycatchers, also have relatively low toe fusion like that of thrushes.

Harrison (1967) suggested that the babbler *Ifrita* from New Guinea is closely related to the blue wren group of *Clytomyias*, *Chenorhamphus*, *Todopsis* and *Malurus* of Australia and New Guinea. I find that all these genera share a high fusion of toes III and IV. In addition, *Ifrita* has a ridged culmen like that of *Clytomyias* and shares the unusual feature of blue feathering on the head with *Todopsis*, *Malurus* and male *Chenorhamphus*. Thus, several characters link *Ifrita* with the malurids, indicating a possible relationship not reflected in traditional classification. *Clytomyias*, *Chenorhamphus*, *Todopsis* and *Malurus* have an unusual gap in the interscapular zone of the spinal feather tract, present also in the Australian grass-wrens (*Amytornis*) and emu-wrens (*Stipiturus*; Harrison 1969); the condition of *Ifrita* in this regard has not been reported. As the relatively terrestrial *Amytornis* and *Stipiturus* have low fusion, caution is necessary in using fusion as a taxonomic character in this group.

Dorst (1960) proposed that the monotypic genera *Tylas* and *Hypositta* from Madagascar belong in the family Vangidae, which is endemic to that island. The high fusion in all these birds is compatible with his suggestion, although high fusion also occurs in other families with which *Tylas* has often been placed, including bulbuls (Pycnonotidae). In *Hypositta*, toe fusion is greater than in typical nuthatches (Ridgway 1904:439; this study), and *Hypositta* is thus more like the vangids in this respect. Also from Madagascar is *Newtonia*, the sole genus of the Muscicapinae outside the Australian region having moderate to high fusion. Although superficial appearances of study skins can be highly misleading concerning evolu-

tionary affinities, *Newtonia brunneicauda* and females of the vangid *Calicalicus madagascariensis* have some resemblance. Further consideration of the affinities of *Newtonia* would be desirable.

The high fusion of *Cyclarhis*, *Vireolanius*, *Vireo* and *Hylophilus* supports the idea that these genera constitute a monophyletic group (Barlow and James 1975, Raikow 1978). Such high fusion is unusual among New World oscines, being known otherwise from *Certhia* and 2 genera of swallows, *Microbates*, *Ramphocaenus*. Vireos thus differ markedly from most New World 9-primaried oscines, including warblers, tanagers, blackbirds and buntings.

Use of the feet.—As relationships between the degree of fusion and use of the feet are not well understood, I have emphasized here the most conspicuous taxonomic differences, for associations between structure and behavior might be most prominent in such cases. My findings support Rüggeberg's (1960) conclusions, based on a much smaller sample of species, that high fusion often occurs in arboreal species and that low fusion is typical for terrestrial species. Bock and Miller (1959) indicated that the high fusion of syndactyly in nonpasserines was advantageous in arboreal perching because the parallel position of the toes applies all the force of flexion directly against a branch; separated toes would presumably be mechanically less efficient. In those climbing oscines with syndactyly, the forward toes are restrained in a roughly parallel orientation that possibly helps to ensure a secure grasp on vertical surfaces.

My observations of live oscines and of published photographs indicate that birds with low fusion vary the spread of the forward toes considerably according to the kind of perch. On the ground or other flat surfaces, these toes are widely separated, presumably providing a stable base for standing or moving. However, on horizontal perches of a small diameter relative to foot size the forward toes are held close together, a position equivalent to that of syndactyly, with presumably similar advantages. On sharply inclined perches of small diameter, toe II of the lower foot is often abducted from III and IV, which are held close together (Leisler 1972; see also Willis 1969, 1972); the application of forces in 2 directions against the perch by toe II, as opposed to III and IV, presumably helps to prevent the foot from slipping down the perch. Leisler (1972) has provided further details on the relationships between toe position and body orientation of small oscines perched on vertical stems.

A lack of absolute associations between degree of syndactyly and use of the feet prevents the use of structure to predict habits of species not studied alive. For example, the climbing Black-and-white Warbler (*Mniotilta varia*) has low fusion, like that of allied nonclimbing parulids (Parkes 1978; this study), in contrast to the moderate to high fusion of many trunk-

climbers in other families. The tree creepers (*Certhia*), which have highly fused forward toes and stiffened tail feathers, are climbers. Because *Orthonyx* from Australia and New Guinea have the same structural characteristics they might be expected also to be climbers: however, *Orthonyx* actually forage terrestrially, propping themselves on the ground with 1 leg and stiffened tail while scratching in the litter with the other foot (Zusi 1978). As another example of absence of absolute associations between toe fusion and degree of arboreality, many arboreal species have only low to moderate fusion, e.g., kinglets (*Regulus*) and New World orioles (*Icterus*). Possibly such arboreal birds with low fusion differ in perching habits from those with high fusion, but evidence is lacking.

Although asynchronous terrestrial gaits (walking and running) are characteristic for terrestrial oscines, and synchronous (hopping) for arboreal species, there are many exceptions (Clark 1975), and degree of toe fusion is not absolutely associated with gait, except that walking is apparently exceptional in oscines with high fusion. Furthermore, no direct association exists between degree of fusion and the ability to hold food with the feet (Clark 1973). Relationships between fusion and uses of the feet may not be apparent in many cases without simultaneously considering many other aspects of structure and behavior.

SUMMARY

The degree of toe fusion, here summarized for the oscine families, probably has only limited taxonomic usefulness, but may serve along with other characters to detect genera possibly needing further systematic study, e.g., *Chlamydochaera*, *Ifrita*, *Newtonia*. Terrestrial species often have lower fusion than do arboreal or climbing species, but there are important exceptions. Low fusion apparently aids balance on flat substrates, whereas high fusion facilitates perching or climbing. The large number of arboreal species with low fusion has not yet been satisfactorily explained.

ACKNOWLEDGMENTS

I thank G. E. Watson, J. Farrand, Jr. and I. C. J. Galbraith for providing access to specimens in their care. R. L. Zusi gave helpful advice and J. A. Slater made useful suggestions on an earlier version of the manuscript. Miss Mary Hubbard prepared the illustration.

LITERATURE CITED

Ames, P. L. 1975. The application of syringeal morphology to the classification of the Old World insect eaters (Muscicapidae). Bonn. Zool. Beitr. 26:107–134.

Barlow, J. C. and R. D. James. 1975. Aspects of the biology of the Chestnut-sided Shrike-vireo. Wilson Bull. 87:320–334.

Bock, W. J. and W. Dew. Miller. 1959. The scansorial foot of the woodpeckers, with comments on the evolution of perching and climbing feet in birds. Am. Mus. Novit. 1931.

Clark, G. A., Jr. 1973. Holding food with the feet in passerines. Bird-Banding 44:91–99.
———. 1975. Additional records of passerine terrestrial gaits. Wilson Bull. 87:384–389.
———. 1977. Foot-scutes in North American oscines. Bird-Banding 48:301–308.
Dorst, J. 1960. A propos des affinities systematiques de deux oiseaux malagaches: *Tylas eduardi* et *Hypositta corallirostris*. L, Oiseau 30:259–269.
Hall, B. P. and R. E. Moreau. 1970. An atlas of speciation in African passerine birds. Br. Mus. (Nat. Hist.), London, England.
Harrison, C. J. O. 1967. The apparent affinities of *Ifrita*. Bull. Br. Orn. Club 87:97–100.
———. 1969. The affinities of the blue wren genus *Malurus* and related genera: with special reference to the grass-wren genus *Amytornis*. Emu 69:1–8.
Leisler, B. 1972. Artmerkmale am Fuss adulter Teich- und Sumpfrohrsänger (*Acrocephalus scirpaceus*, *A. palustris*) und ihre Funktion. J. F. Orn. 113:366–373.
Morony, J. J., Jr., W. J. Bock and J. Farrand, Jr. 1975. Reference list of the birds of the world. Dept. Ornithology, Am. Mus. Nat. Hist., New York, New York.
Parkes, K. C. 1978. Still another parulid intergeneric hybrid (*Mniotilta* × *Dendroica*) and its taxonomic and evolutionary implications. Auk 95:682–690.
Raikow, R. J. 1978. Appendicular myology and relationships of the New World nine-primaried oscines (Aves: Passeriformes). Bull. Carnegie Mus. Nat. Hist. 7:1–43.
Rand, A. L. and M. A. Traylor, Jr. 1953. The systematic position of the genera *Ramphocaenus* and *Microbates*. Auk 70:334–337.
Ridgway, R. 1901–07. The birds of North and Middle America. U.S. Natl. Mus. Bull. 50, Pts. I–IV.
Rüggeberg, T. 1960. Zur funktionellen Anatomie der hinteren Extremität einiger mitteleuropäischer Singvogelarten. Z. Wiss. Zool. 164:1–106.
Willis, E. O. 1969. On the behavior of five species of *Rhegmatorhina*, ant-following antbirds of the Amazon Basin. Wilson Bull. 81:363–395.
———. 1972. The behavior of Spotted Antbirds. Ornithol. Monogr. No. 10.
Zusi, R. L. 1978. Notes on song and feeding behaviour of *Orthonyx spaldingii*. Emu 78:156–157.

BIOLOGICAL SCIENCES GROUP, UNIV. CONNECTICUT, STORRS, CONNECTICUT 06268. ACCEPTED 25 APR. 1980.

SEVENTH INTERNATIONAL CONFERENCE ON BIRD CENSUS WORK AND FIFTH MEETING OF THE EUROPEAN ATLAS COMMITTEE

An international conference for those involved or interested in bird census and/or atlas work will convene 8–12 September 1981 at the Universidad de León, Spain. For further information write: Prof. Francisco Purroy, Departamento de Zoologia, Facultad de Biologia, León, Spain.

Wilson Bull., 93(1), 1981, pp. 77–84

ENVIRONMENTAL EFFECTS ON ROOSTING BEHAVIOR OF CHIMNEY SWIFTS

Richard M. Zammuto and Edwin C. Franks

The Chimney Swift (*Chaetura pelagica*) is widespread and abundant in eastern North America. The lengthy migration and long-unknown wintering grounds of this species early attracted attention, but detailed ecological research on this species began only in the middle of this century (Fischer 1958). Others have focused on responses by swifts to environmental conditions. Ramsey (1970), for example, studied the effect of changing ambient temperatures upon internal body temperatures, and Michael and Chao (1973) showed associations between roosting behavior, time of sunset and light intensity. Here we relate roosting and other behaviors to several environmental variables.

STUDY AREA AND METHODS

Our studies were conducted in Macomb, McDonough Co., Illinois. Midsummer daily temperatures range from 18–36°C. The center of the city has several blocks of contiguous 3- to 5-story buildings; the central area is surrounded on each side by about 10 blocks of 1- to 3-story homes averaging 10 m apart. Because Macomb is surrounded by cultivated farmland and is the largest city (population 23,000) in a 60 km radius, it holds the major portion of the Chimney Swift population in the area.

The first Chimney Swifts usually arrive in mid-April. Numbers are low until late April and early May, when the first large flocks are seen. The city contains a large population of swifts (1000–3000) until nest-building begins in late May, when numbers decline to fewer than 1000. During June and July, most chimneys with swifts contain 1 breeding pair with occasional visitors or nest helpers (see Dexter 1952, 1974). A few chimneys contain flocks consisting of non-breeding swifts (up to 300) or both a nesting pair and a flock (Zammuto and Franks 1978). Nesting occurs throughout the city from early June to August. Population numbers peak during September and slowly decrease until mid-October when all the swifts are gone for the winter.

Roosts of 6 or more individuals were analyzed. We located most roost-sites from a car at dusk by watching for circling flocks of swifts. Individual roost-sites were studied for several mornings and/or evenings. Those sites used most by swifts were observed most often.

A photometer placed on top of a car roof facing the open sky was used to measure light intensity. For each foot-candle (fc) change in light intensity during exit or entrance by swifts, the time and number of birds (tallied on hand counter) that left or entered a chimney were recorded. These data were tested using exponential curvilinear correlation and regression analyses.

The times when the majority of swifts left or entered a roost-site were determined with a stopwatch and an average time, designated as the time of peak exit or entrance, was computed. Temperatures and wind velocities were measured 1.5 m above ground near each roost-site. Cloud cover was estimated to the nearest 5%. These measurements and the times of sunrise and sunset were examined in relation to the time of peak exit and entrance at the roost-site using multiple regression and correlation analyses. The mean difference between time of

peak exit and time of sunrise and between time of peak entrance and time of sunset were analysed with regard to sky haziness and precipitation using *t*-tests. Sky haziness indicated that a fair sky was somewhat hazy, not clear blue. Precipitation was recorded as present or absent. Throughout this report, means appear with ±1 SD unless otherwise indicated.

RESULTS AND DISCUSSION

The mean number of Chimney Swifts recorded leaving a roost-site (N = 32) was 70 on 203 mornings, and the mean number entering was 83 on 166 evenings. A total of 224 flock departures or entries was observed at the 32 different chimneys. Of the 224, 65% of the departures or entries were of less than 100 individuals (Fig. 1).

Behavior at departure.—The swifts could usually be heard calling inside the chimney when we arrived at the roost 0.5 h before daylight. The calling became louder as daylight approached (about 0.2 fc), and continued during exit by swifts.

On many mornings, 1–10 swifts arrived at a roost-site about 20 min before any swifts left. Sometimes they circled the chimney and then flew away but more often they entered the chimney. The roosting birds called more loudly if any of these swifts entered the chimney, but the calling subsided after about 15 sec.

Swifts departed roost-sites singly or in small groups, almost always in a steady flow at rates of 4–150 per min. Sometimes a 30-min interval occurred between departure of 2 substantial portions of a flock.

Morning returns to roost-site.—After swifts left a chimney, some birds reentered on about 50% of the mornings. About 18% of 14,144 departing birds reentered within 30 min after first departure, and 3% reentered between 30 and 60 min. On about 3% of the mornings, more swifts entered a chimney than had left it only minutes before.

Swifts often circled the chimney without reentering for many minutes. When 1 circling swift entered, many other circling birds immediately followed in quick succession; the rest circled without reentering for several more minutes until another bird entered, followed by another portion of the group.

Weather conditions seemed to affect reentry into the roost. On cold or rainy mornings, over 90% of the swifts that left a chimney reentered it within 30 min. On these mornings, some were reentering while others were leaving. A shortage of insects in the air may also cause reentry. The number of insects in flight was likely very high at daybreak but probably declined sharply after sunrise (McClure 1938; Glick 1939, 1957). Reduced aerial prey may have caused the swifts to reenter the roost-site at sunrise (on the average of 11 min after departure) where they remained until later in the morning.

Evening observations of behavior.—Entry into the roost in the evening

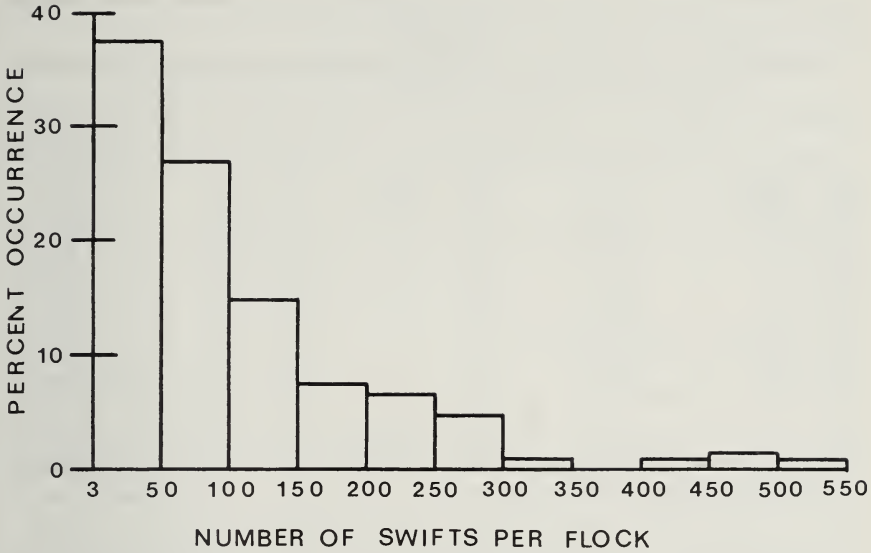


FIG. 1. Size of 224 flocks.

is described in detail by various authors (James 1950, Zammuto 1978). Often more than 50 swifts per min entered the chimney if light levels dropped to 0.5 fc with most of the flock still outside. Reentry rate in the morning was usually lower, so we believe approaching darkness is a major stimulus for entering the roost at dusk. However, as reported by Calhoun (1938), there were many evenings when only a few swifts were seen at any one time near a roost-site. As soon as they entered, additional small groups moved into the area and entered the chimney until the whole flock was inside.

Alterations in roosting behavior.—Various human-related activity disrupted swift roosting patterns. Fumes from furnaces, noises from loud vehicles, slamming doors and voices sometimes caused the swifts to leave the roost early, or caused circling swifts to disperse from the roost-site. On 60% of the summer evenings loudly calling swifts flying near roost-sites seemingly caused all the swifts in the area to disperse, although most usually returned within 3 min.

On nearly 50% of the evenings, late-arriving individual swifts circled the roost a few times but then flew off (Coffey 1936). Koskimies (1950) felt that such behavior in the Common Swift (*Apus apus*) indicated it was too dark for the swifts to see well enough to enter the roost, and thus swifts overtaken by nightfall spent the night on the wing.

TABLE 1

MONTHLY MEAN LIGHT INTENSITY (FOOT-CANDLES) WHEN THE SWIFTS ENTERED THE ROOST

Date	No. swifts	No. evenings observed	Mean ± SE	Light intensity mode
Sept. 1976	207	3	0.6 ± 0.35	0.5
Oct. 1976	623	8	0.7 ± 0.17	0.5
April 1977	401	4	0.5 ± 0.28	0.5
May 1977	1937	18	1.8 ± 0.30	0.5
June 1977	2853	25	2.7 ± 0.23	0.5
July 1977	2474	14	3.3 ± 0.33	0.5
Aug. 1977	886	10	3.5 ± 0.44	1.5
Sept. 1977	1934	19	1.0 ± 0.14	0.5
Oct. 1977	183	2	1.1 ± 0.37	0.5
Total	11,498	103	overall $\bar{x}$ = 1.7 ± 1.2[a]	0.6

[a] Standard deviation of the 9 monthly means shown.

Light intensity.—Morning departure of the swifts was more widely distributed at very low light intensities than was evening descent. Based on 12,430 birds, 70% left the chimney during light of 0 and 7 fc, while a similar percentage of 11,498 birds entered between a more restrictive 0 and 2 fc.

Light intensity was negatively correlated with the number of swifts leaving the roost each morning ($r = -0.87$, $P < 0.001$) and entering the roost each evening ($r = -0.63$, $P < 0.001$). The regression formula for the

TABLE 2

MONTHLY MEAN LIGHT INTENSITY (FOOT-CANDLES) WHEN THE SWIFTS LEFT THE ROOST

Date	No. swifts	No. mornings observed	Mean ± SE	Light intensity mode
Oct. 1976	634	11	6.7 ± 0.62	0.5
April 1977	391	3	8.0 ± 1.56	2.5
May 1977	1668	16	2.3 ± 0.21	1.5
June 1977	2104	25	3.7 ± 0.24	2.5
July 1977	2982	17	7.0 ± 0.46	2.5
Aug. 1977	1900	13	4.1 ± 0.49	3.5
Sept. 1977	2185	16	8.1 ± 0.44	7.5
Oct. 1977	394	4	4.4 ± 0.57	2.5
Total	12,430	105	overall $\bar{x}$ = 5.5 ± 2.2[a]	2.9

[a] Standard deviation of the 8 monthly means shown.

TABLE 3

EQUATIONS AND CORRELATIONS SHOWING THE EFFECT OF ENVIRONMENTAL VARIABLES ON THE MEAN TIME OF PEAK EXIT AND ENTRANCE AT THE ROOST-SITE

	Exit			Entrance		
Independent variable	Equation[a]	Coefficient of determination[b]	No. mornings	Equation[a]	Coefficient of determination[b]	No. evenings
Time of sunrise	$Y = -0.37 + 1.0X$	0.96***	114			
Time of sunset				$Y = 0.40 + 1.0X$	0.98***	114
Temperature (°C)	$Y = 7.1 - 0.072X$	0.43***	114	$Y = 18.2 + 0.092X$	0.32***	114
Wind speed (km/h)	$Y = 6.1 - 0.044X$	0.05*	113	$Y = 20.1 + 0.06X$	0.05**	114
Percent cloud cover	$Y = 6.0 - 0.002X$	0.02	109	$Y = 20.2 + 0.002X$	0.01	112

[a] Where Y is the mean time (24-h clock, CDT) of peak exit from or entrance into the roost-site and where X is the independent variable listed.

[b] Levels of significance as determined by F tests: $*P < 0.05$, $**P < 0.01$, $***P < 0.001$.

number of swifts (Y) leaving and entering the roost with respect to each level of light intensity (fc) was $Y = 17.3e^{-0.050^{fc}}$ at dawn and $Y = 13.1e^{-0.131^{fc}}$ in the evening.

The swifts entered the roost at significantly higher light intensities in the warmer months (May through August) than in the colder months (April, September, October) ($t = 5.68$, df = 7, $P < 0.001$) (Table 1). In a Texas study by Michael and Chao (1973), May through August was also when swifts entered the roost at higher mean light intensities, although in their study, light intensities at entrance were much higher (ranging between 2.0 and 14.2 fc, $\bar{x} = 5.9 \pm 3.7$) than the ones we observed (0.5–3.5 fc, $\bar{x} = 2.0 \pm 1.1$; for 1977, Table 1). Mean monthly light intensities at which swifts left roost-sites are shown in Table 2.

Sunrise and sunset.—The times of sunrise and sunset were more closely associated with the mean time of peak exit or entrance at the roost than temperature, wind speed, or cloudiness (Table 3).

Swifts left the roost about 11 min before sunrise and entered it about 21 min after sunset (Table 4). There was less than a 10 min difference among monthly means. In spring and summer in Texas, swifts entered the roost much sooner after sunset ($\bar{x} = 14 \pm 2$ min, range 12–16 min) (Michael and Chao 1973) than did swifts in our study for all months.

Temperatures.—Swifts left the roost significantly later and entered it

Table 4

Times Before Sunrise and After Sunset When Swifts Left and Entered the Roost-site at the Fastest Rate

Date	No. mornings	Monthly mean minutes before sunrise ± SE	No. evenings	Monthly mean minutes after sunset ± SE
Sept. 1976	11	9.8 ± 1.8	11	22.4 ± 1.3
Oct. 1976	11	11.7 ± 1.7	7	22.6 ± 1.7
April 1977	3	7.7 ± 2.9	4	21.8 ± 0.8
May 1977	15	17.3 ± 0.9	18	23.1 ± 1.3
June 1977	24	12.2 ± 1.7	27	21.9 ± 1.2
July 1977	17	10.7 ± 0.9	15	18.0 ± 2.1
Aug. 1977	13	12.3 ± 2.7	13	17.1 ± 0.8
Sept. 1977	16	9.0 ± 1.2	18	18.6 ± 0.7
Oct. 1977	4	8.9 ± 1.9		
Total	114	overall $\bar{x}$ = 11.1 ± 2.8[a]	total 113	overall $\bar{x}$ = 20.7 ± 2.4[b]

[a] Standard deviation of the 9 monthly means shown.
[b] Standard deviation of the 8 monthly means shown.

significantly earlier on colder days (Table 3). Koskimies (1950) found that *A. apus* did not leave the roost-site until the air temperature was high enough for normal numbers of flying insects to be available. Chimney Swifts may behave similarly. In southern Texas, Glick (1939, 1957) found that the greatest numbers of insects were in the air at 25°C, and that numbers of insects decreased considerably below 18°C; very few were flying at temperatures below 15.6°C.

Wind speed, cloud cover and haziness.—With higher wind speeds, the swifts leave the roost earlier in the morning and stay out later in the evening (Table 3). Numbers of flying insects may be an important factor; Glick (1939, 1957) found that the abundance of insects in flight decreased as winds dropped below 8 km/h. Therefore, fewer insects were flying and presumably less food was available for swifts on calmer days. It may be more advantageous to be roosting when the food supply reaches some lower threshold. Neither cloud cover (Table 3) nor sky haziness had significant ($P > 0.05$) effects on the time of peak exit or entrance.

Precipitation.—Rainfall significantly delayed the time of peak exit from the roost (mean exit time on 10 rainy mornings = 0.3 min before sunrise, mean on 103 fair mornings = 12.5 min before sunrise, $P < 0.001$). On rainy mornings, the swifts usually stayed in the chimney until the rain stopped, but if they did depart in the rain, most quickly reentered. In sporadic rain, the reentry corresponded to the periods of rain. Rainy weather also delayed the onset of daily activity in *A. apus* (Koskimies 1950), probably due to a reduction of the food supply. If the rain continued for several consecutive

days, the Chimney Swifts did not return to the roost in the morning after the first 2 days. They were probably forced to hunt in the poor weather to keep from starving, or moved elsewhere.

On 5 days, Chimney Swifts circled roost-sites when summer afternoon thunderstorms threatened. During most storm threats, Chimney Swifts flew low, resuming their normal clear day flying height when the threat passed as observed for Black Swifts (*Cypseloides niger*) (Rathbun 1925). Between intermittent rain showers, the swifts we were studying usually flew in small flocks, flying lower than usual. They may have been following their food supply; Koskimies (1950) found that many insects were washed down to the ground by rain. Some swifts in our study were repeatedly observed flying close to lawns when it rained (Zammuto and Franks 1979). *A. apus* reduced foraging activity in rain (Koskimies 1950, Lack and Lack 1951).

When it rained, Chimney Swifts entered the roost-site earlier (mean of 8 rainy evenings = 16.3 min after sunset, mean of 104 fair evenings = 20.9 min after sunset, $P < 0.05$). On most rainy evenings about 10% of any flock entered the roost 30 min before the rest of the birds. If the rain stopped after such early entrances some birds left the roost.

James (1950), Bowman (1952) and Fischer (1958) noticed increases, but Dexter (1966, 1968) noticed decreases in roosting flock sizes during prolonged, cool, rainy periods. In our study, swift numbers increased at 10 roost-sites during 10 such periods. Some flock sizes doubled, reaching 200 or more birds. Since in the summer months these added birds in our study were probably not migrants (Zammuto 1978), we postulate that they moved from smaller roosts. Presumably, loss of body heat would be minimized when many swifts formed tight roosting clusters than when only a few swifts were present. This would allow the swifts to survive longer without food since they stayed in the roost-site during cool, rainy weather. Dexter (1966) noted that flocks he observed decreased in numbers in inclement weather and he hypothesized that absent birds were roosting in warmer chimneys elsewhere. Our experience suggests that they were in a larger roost, but we never studied small roosts during rainy periods to see if swift numbers decreased.

SUMMARY

Roosting of Chimney Swifts was studied in relation to several environmental variables in September and October 1976 and April through October 1977. An average of 70 swifts were recorded leaving and 83 entering 32 different roost-sites on 203 mornings and 166 evenings. Of 224 flocks, 65% numbered below 100 individuals. About 18% of the swifts that left the roost-site at dawn returned to it to reenter around sunrise. In the morning, 70% of the swifts left the chimney during light intensities of 0–7 fc, but in the evenings 70% entered between a more restrictive 0 and 2 fc. Swifts left the roost-site at 5.5 ± 2.2 fc, 11.1 ± 2.8 min before sunrise and entered at 1.7 ± 1.2 fc, 20.7 ± 2.4 min after sunset. Light intensity, time of

sunrise and sunset, temperature, wind speed and precipitation were all associated with the time of departure from and entrance into the roost-site. Swifts left the roost-site later and entered it earlier on colder days, on days with precipitation, and on calmer days. The effect of sky haziness and cloud cover upon time of peak exit and entrance was not significant. All the environmental variables reported to affect flying insect abundance were similarly associated with swift activity patterns.

ACKNOWLEDGMENTS

Donald Campbell and Robert Beason assisted with the statistical analyses, and Tate Lindahl helped with the computer programming. Julie Zammuto helped in the field, and she and Judy Zielinski provided valuable secretarial assistance. Charles Collins, Ralph Dexter, Gary Schnell and Jerrold Zar suggested improvements for earlier drafts.

LITERATURE CITED

Bowman, R. I. 1952. Chimney Swift banding at Kingston, Ontario from 1928 to 1947. Can. Field-Nat. 66:151–164.

Calhoun, J. B. 1938. 1938 Swift banding at Nashville and Clarksville. Migrant 9:77–81.

Coffey, B. B. 1936. Chimney Swift migration at Memphis. Migrant 7:77–82, 96–98.

Dexter, R. W. 1952. Extra-parental cooperation in the nesting of Chimney Swifts. Wilson Bull. 64:133–139.

———. 1966. Analysis of Chimney Swift returns at Kent, Ohio, in 1964 and 1965, with notes on a declining nesting population. Bird-Banding 37:120–121.

———. 1968. Analysis of the 1966 and 1967 returns of Chimney Swifts at Kent, Ohio. Bird-Banding 39:56–57.

———. 1974. Unusually large numbers of Chimney Swifts at a nest. Bird-Banding 45:365.

Fischer, R. B. 1958. The breeding biology of the Chimney Swift, *Chaetura pelagica* (Linnaeus). N.Y. State Mus. Bull. 368.

Glick, P. A. 1939. The distribution of insects, spiders and mites in the air. U.S. Dept. Agric. Tech. Bull. 673.

———. 1957. Collecting insects by airplane in southern Texas. U.S. Dept. Agric. Tech. Bull. 1158.

James, P. 1950. Spring flocking of Chimney Swifts (*Chaetura pelagica* Linnaeus) at Cornell University. Bird-Banding 21:9–11.

Koskimies, J. 1950. The life of the Swift, *Micropus apus* (L.) in relation to the weather. Ann. Acad. Sci. Fennica 15:1–151.

Lack, D. and E. Lack. 1951. The breeding biology of the Swift, *Apus apus*. Ibis 93:501–548.

McClure, H. E. 1938. Insect aerial populations. Ann. Ent. Soc. Am. 31:504–513.

Michael, E. D. and W. H. Chao. 1973. Migration and roosting of Chimney Swifts in east Texas. Auk 90:100–105.

Ramsey, J. J. 1970. Temperature changes in Chimney Swifts (*Chaetura pelagica*) at lowered environmental temperatures. Condor 72:264–265.

Rathbun, S. F. 1925. The Black Swift and its habits. Auk 42:497–516.

Zammuto, R. M. 1978. Seasonal activity of the Chimney Swift (*Chaetura pelagica*) population in Macomb, Illinois. M. Sc. thesis, Western Illinois Univ., Macomb, Illinois.

——— and ———. 1979. Chimney Swifts apparently feeding near surfaces of lawns and from trees. Inland Bird Banding 51:72–73.

——— and E. C. Franks. 1978. Forty adult Chimney Swifts at an active nest. Bird-Banding 49:278–279.

DEPT. BIOLOGICAL SCIENCES, WESTERN ILLINOIS UNIV., MACOMB, ILLINOIS 61455. (PRESENT ADDRESS RMZ: DEPT. ZOOLOGY, UNIV. WESTERN ONTARIO, LONDON, ONTARIO N6A 5B7 CANADA.) ACCEPTED 20 DEC. 1979.

Wilson Bull., 93(1), 1981, pp. 85–92

GENERAL NOTES

Observation of a brood of Sharp-shinned Hawks in Ontario, with comments on the functions of sexual dimorphism.—The Sharp-shinned Hawk (*Accipiter striatus*) exhibits the greatest "reversed" sexual dimorphism in size of any North American bird, with males averaging 100 g and females 170 g (Mueller and Berger, Auk 87:452–457, 1970). Of the several, controversial hypotheses to explain the extent of sexual dimorphism in raptors, that of Snyder and Wiley (Ornithol. Monogr. 20, 1976) is perhaps most amenable to verification. Snyder and Wiley have suggested that food stress late in the period of dependency of the young has acted to select for adults of greatly different body sizes, and thus different feeding niches. This increases the range of size of prey available to maintain the adults and their rapidly growing young. Casual observations of breeding Sharp-shinned Hawks and small bird populations in Ontario led us to question this hypothesis and served as the inspiration for this study.

The senior author is preparing an extensive discussion of the hypothesis of Snyder and Wiley. The purpose of this paper is simply (1) to present our intensive observations of 1 brood of Sharp-shinned Hawks, (2) to compare our results with those of 3 nests studied by Snyder and Wiley, and (3) to offer alternative explanations for some of the data. Our observations are unique in the amount of time and effort expended in observations during the post-fledgling period and in that ours is the first detailed study from eastern Canada, which appears to be the center of abundance of the species (Bent, U.S. Natl. Mus. Bull. 167, 1937).

We found a brood of 4 Sharp-shinned Hawks (3 females and 1 male) near their nest in Burpee Township, Manitoulin Island, Ontario, on 22 July 1977. We began observations on the brood that afternoon and continued daily until noon on 8 August when we had to depart. Two to 5 observers (usually 3) watched for 6.7 ± 2.67 (SD) h per day with the least observation (1.95 h) on 2 August, when it rained most of the day. The nest was about 11 m up in a white spruce (*Picea glauca*) in a grove dominated by both this species and northern white cedar (*Thuja occidentalis*), with scattered small groups of quaking aspen (*Populus tremuloides*) and an occasional balsam fir (*Abies balsamea*), white birch (*Betula papyrifera*) and white pine (*Pinus strobus*). The nest was in the southwest corner of the grove about 35 m from the western edge and 30 m from the beach of Lake Huron. The grove extended about 130 m north and 200–350 m east of the nest, the edge was irregular, and a narrow strip of trees connected the grove to 2 larger forests to the east and north. The area surrounding the grove is locally called a "prairie," an open parkland covered with lichens, sparse grasses and some bare dolomite rock. Individual and small groups of trees, scattered through the prairie, formed 5–20% of the vegetative cover.

At least 1 observer remained near the young; the other observers were stationed at points which offered the best view of approaching adults. The young habituated to our presence rapidly and would tolerate approach to within less than 5 m after the second day of observations. The adult female also habituated rapidly. She perched quietly near us on a number of occasions. The adult male flew within 10 m of us several times, but was not observed perching near us. The young usually occupied rather exposed perches, either in aspens or dead trees of various species, although well-fed young were occasionally found on secluded perches. The center of activity of the young, as they grew older, moved northward from the nest and we moved our observation posts accordingly.

On 28 July, the young appeared to have achieved full feather growth and flight skills comparable to those of the adults; identification of age was possible only if we saw the plumage or heard begging calls. Camp (*in* Platt, unpubl. M.S. thesis, Brigham Young Univ., Provo, Utah, 1973) indicates that full feather growth is attained at an age of 38–40 days. We

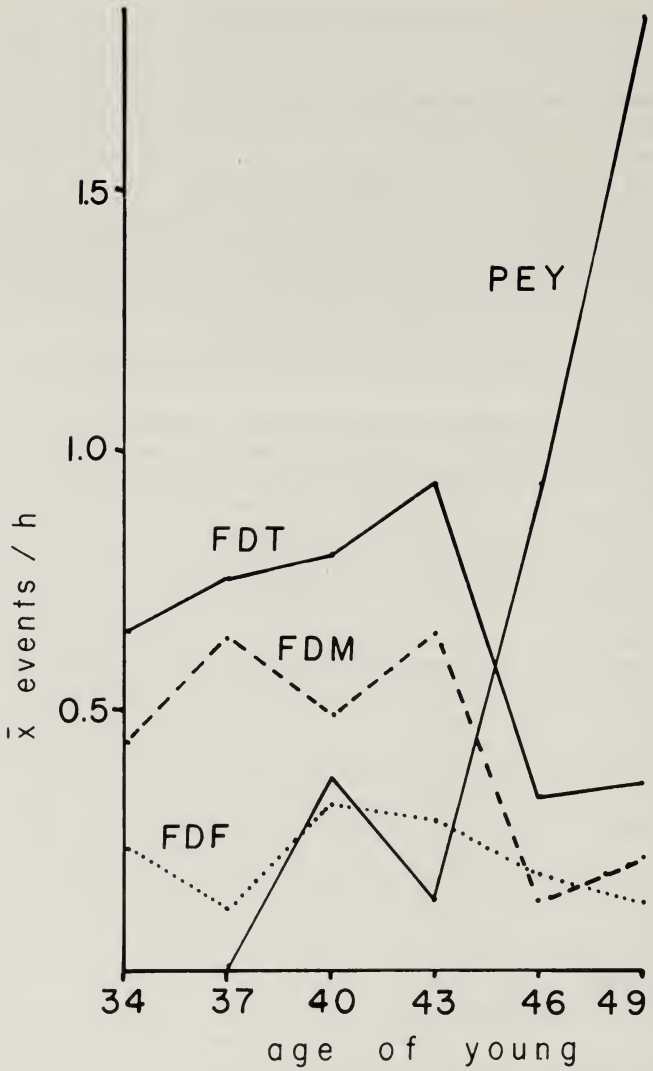


FIG. 1. Mean prey deliveries per h by the adults and mean "predatory episodes" per h involving young. FDF: food deliveries by the female. FDM: food deliveries by the male. FDT: sum of food deliveries for both sexes. PEY: predatory episodes involving young (see text).

thus estimated the age of our birds as 33 days when we discovered them on 22 July and that the females had left the nest about 6 days and the male about 9 days before we began observations.

Identification of prey items was rarely possible, particularly since most prey items were

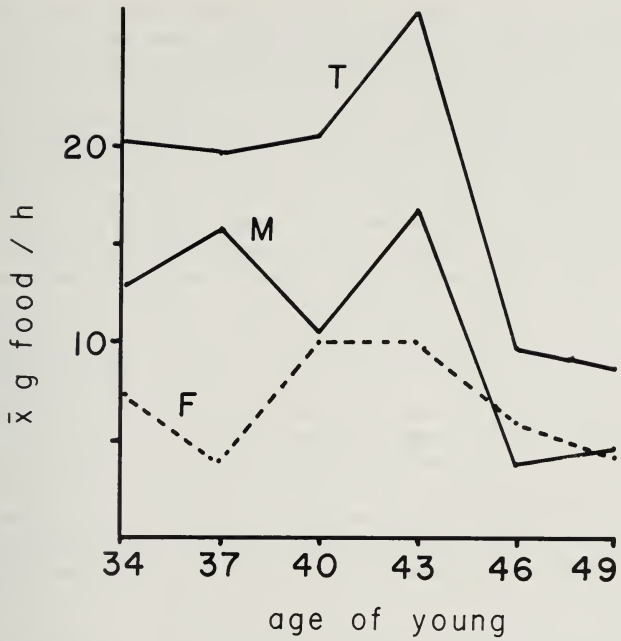


FIG. 2. Mean estimated g of food delivered per h by the adults; F: delivered by female, M: delivered by male, T: sum of the 2.

delivered plucked and remains were rarely found. If we obtained a sufficiently good look at the prey as it was being carried by the adult, we estimated its size and weight.

We did not attempt to census prey-bird populations in the range of the hawks, but a subjective judgement is that the populations were about the same as on 2 previous visits to Manitoulin at the same time of year.

Food deliveries and behavior of the adults.—In our 120.5 h of observation, there were 73 deliveries of food by the adults, 40 by the male, 23 by the female and in 10 cases we could not determine the sex of the adult. In 34 of the 73 deliveries (male 22, female 10, unknown sex 2), the prey item was seen sufficiently well, or sufficient remains were found to permit estimation of size. The 22 such prey items delivered by the male had a mean weight of 26 ± 14.8 g (range 10–80 g). The 10 items delivered by the female had a mean weight of 35 ± 21.5 g (range 10–90 g). The difference in weight of prey delivered by the sexes was not statistically significant (t-test, $P > 0.26$, 1-tailed).

To examine changes in the feeding rates by the adults, we divided our 18 days of observations into 6 three-day intervals, thus insuring a reasonable amount of observation time per interval (mean 19.9 h, range 14.0–25.9 h). Within a 3-day interval, food deliveries by adults of unknown sex were assigned to the sexes in proportion to the deliveries by adults of known sex. Weights of prey items not seen were assigned to the mean weight of prey delivered by that sex. The male made 0.53/h food deliveries during the first 12 days of study and only 0.18/h during the last 6 days (Fig. 1). The female showed less temporal change in food

deliveries: 0.24/h for the first 12 days and 0.16/h for the last 6 days. The estimated weight of food delivered per h shows similar trends: 13.6 g/h by the male and 7.7 g/h by the female during the first 12 days and 4.2 g/h by the male and 5.0 g/h by the female during the last 6 days (Fig. 2). There was a precipitous decline in total food deliveries between the end of the sixth week of age of the young and the beginning of the seventh week: 65% fewer deliveries per h and 63% fewer g/h. Daily mean deliveries/h for this 6-day period, when the young were 42 through 47 days old were: 1.05, 0.63, 1.54, 0.42, 0.25, 0.32. The dramatic drop from 1.54 deliveries per h to 0.42/h is further intersting because the latter day (3 August) marked the first easily noticeable influx of migrant passerines (mostly warblers) into the area.

The adult female was observed to loiter in the nest grove on 13 occasions for a mean of 0.83 ± 0.67 h. These 13 occasions of loitering occurred throughout our period of observation and as late as 7 August. The female may have spent even more time in the nest grove. She usually flew below canopy for some distance before relinquishing food to the young and then exited the grove at low altitude, sometimes unobserved. The male either dropped prey to the young above canopy, or dipped briefly below the treetops. The male was known to loiter in the grove on only 3 occasions for a mean duration of 0.15 ± 0.08 h. Neither adult showed any behavior which appeared defensive of the young in our presence.

We observed the female apparently hunting on 2 occasions, about 0.7 and 1.3 km from the nest. She was once observed carrying food 1.2 km from the nest. The male was never observed hunting. On the basis of our observations, we suspect that most of the hunting was done more than 1.5 km from the nest, although prey appeared to be abundant in the immediate vicinity. Chipping Sparrows (*Spizella passerina*), Yellow-rumped Warblers (*Dendroica coronata*) and American Redstarts (*Setophaga ruticilla*) were observed with fledged young within 20 m of the nest.

Behavior of the young.—The first predatory efforts by the young were observed on 29 July, when they were 40 days old and food deliveries by the adults were quite frequent (Fig. 1). Of the 80 "predatory episodes by young" depicted in Fig. 1, 52 were stoops or obvious pursuit flights at prey hidden from our view by vegetation. Of these 52, 23 were definitely unsuccessful, and for the other 29 cases we could not determine the outcome. During the last few days of our observations, young would often disappear for several hours, apparently hunting. Our efforts to follow and find such young were rarely successful, probably because of the extremely cryptic behavior of the birds. Distress calls of potential prey birds account for 16 episodes. In 2 episodes, young birds were seen apparently eating a tiny item (grasshoppers were extremely abundant in the prairie surrounding the nest grove). On 1 other occasion, 3 young were flushed from the ground by one of us twice in 3 minutes. The young remained together and their behavior strongly suggested that one had food but the dense vegetation prevented us from confirming this. No food delivery by an adult had occurred during the previous 3.13 h. On 9 occasions, we saw the bird at which the young hawk stooped. These included 4 pursuits of Gray Jays (*Perisoreus canadensis*), 2 stoops at small passerines, 1 at an unidentified warbler, 1 at a Yellow-rumped Warbler and 1 at a Common Flicker (*Colaptes auratus*). The most spectacular pursuit of prey occurred on 7 August, when we saw the young male suddenly leave a perch about 15 m up in a dead white pine. Accelerating rapidly with flicking wing-beats, he intercepted a flying warbler about 80 m away, missing by less than 30 cm as the warbler dived. The hawk wheeled and plunged after the warbler which disappeared into a spruce. We did not observe any successful capture of prey by the young, but the hawks had ample opportunities when they were not under surveillance by us. During the last few days of our observations, known positions of individual young were sometimes more than 1.5 km apart and on our last day 1 young disappeared 2 km to the north, flying high, and did not return during our last 40 min of observation. It is possible that we witnessed the departure of 1 young.

On 8 August, our last day of observations, all 4 young were under surveillance for only 0.7% of the 5.05 h of observation. Three young were under surveillance 29.7% of the time, 2 young 40.1%, 1 young 37.0% and 12.3% of the time no young were seen.

Discussion.—The 65% decline in food deliveries by the adults that occurred between 42–44 and 45–47 days of age of the young is far too sudden to be explained by a decline in prey availability or vulnerability. Furthermore, we noted a marked influx of migrant passerines into the area on day 44, just when the decrease in prey deliveries began. The decrease can be explained by a reduction in hunting by the adults. Sharp-shinned Hawks become independent of the parents at an age of about 7 weeks (Platt 1973, Snyder and Wiley 1976). A reduction in food deliveries by the adults 6 days before the young become independent and the continued begging of the young is consonant with the parent-offspring conflict hypothesis of Trivers (Am. Zool. 14:249–264, 1974). During the "weaning" period the attempts of the offspring to maximize their inclusive fitness come into conflict with that of the parents. The young selfishly demand more care than the parents, selfishly, should provide. Davies (Ibis 120:509–514, 1978) has suggested that if parents time the decline in feeding rates in response to cues from the young, they are open to being "cheated" in the conflict of maximizing fitness. If, on the other hand, the adults feed for a fixed period irrespective of the performance of the young in feeding themselves, young would be lost in times of food scarcity. The optimal strategy would involve flexibility in the behavior of the adults with parental care being prolonged when food is scarce. Davies presents the results of several studies which indicate that the length of the parental care period in birds is affected by the availability of food. We believe that this is the key to the understanding of the differences in feeding behavior of adults observed at various nests.

Newton (J. Zool. London 184:465–487, 1978), in summarizing his observations of the Sparrowhawk (*A. nisus*), suggested that the male usually brings as much food to the young as it can and that the female is induced to hunt chiefly when the efforts of the male do not meet the needs of the young. Newton noted that female *A. nisus* often loiter in the vicinity of the nest, a phenomenon observed by us, and by Platt (1973) in *A. striatus*. The available data on the Sharp-shinned Hawks are in complete agreement with Newton's hypothesis. The male Puerto Rican Sharp-shinned Hawk of Snyder and Wiley (1976) was able to provide adequate food for his family, and the female did no hunting (at least not to provide food for the young). For the spruce-fir brood of Snyder and Wiley and our Manitoulin Island brood, the male could not provide all of the needs of the young, and the female did some hunting. In the case of the riparian canyon brood of Snyder and Wiley, which we readily agree was under conditions of food stress, the female had to do considerable hunting to help feed the young. The same was possibly true of the oak-juniper brood of Snyder and Wiley, although the data are limited.

The peak in food deliveries to the Puerto Rican brood of Snyder and Wiley occurred during week 5 (the week after fledging) with a sharp drop in week 6 and little further decline in week 7. The spruce-fir brood of Snyder and Wiley showed a peak in week 4, with a considerable and steady decline through week 5 and weeks 6 and 7 (the 2 weeks were lumped because of limited observations). However, if we look at the amount of food delivered per young, the spruce-fir brood also shows a peak during week 5 (1 young disappeared at the end of the fourth week, cause unknown). A recalculation of the data shown in Fig. 2 into weekly intervals shows that our Manitoulin Island brood received the same amount of food during the last 3 days of week 5 (21.2 g/h) as they did in week 6 (21.3 g/h) with a sharp drop to 11.5 g/h in week 7. The lack of a peak in week 5 for our brood might possibly be due to the fact that we did not begin observations until the last 3 days of that week. Another possible partial explanation for the differences observed between nests in the temporal pattern of food deliveries is in the sex ratios of the brood. Newton (1978) found no difference in the

Table 1

Per Cent Distribution of Size Classes of Prey Taken and Prey Available

		Size class[a]						
		N	1	2	3	4	5	6
Prey taken	♂	124	11.3	33.1	40.3	11.3	0.8	3.2
(Storer 1966, Table 5)	♀	125	1.6	21.6	37.6	23.2	1.6	8.0
Spruce-fir nest (Snyder and Wiley 1976)								
Prey taken	♂	68	0	48.5	47.1	4.4	0	0
(Table 5)	♀	8	0	50.0	50.0	0	0	0
Prey available (Table 17)			14.3	61.0	12.3	5.6	2.9	3.8
Riparian canyon nest (Snyder and Wiley 1976)								
Prey taken	♂	36	22.2	58.3	16.7	2.7	0	0
(Table 5)	♀	15	0	20.0	6.7	26.7	26.7	20.0
Prey available (Table 17)			22.0	44.9	7.1	9.5	7.3	9.3
Oak-juniper nest (Snyder and Wiley 1976)								
Prey taken	♂	19	0	36.8	63.2	0	0	0
(Table 5)	♀	4	0	25.0	25.0	0	25.0	25.0
Prey available (Table 17)			14.3	40.7	20.5	12.1	5.1	7.2
Manitoulin Island	♂	22	0	18.2	50.0	22.7	4.5	4.5
Prey taken	♀	10	0	10.0	40.0	10.0	30.0	10.0

[a] The size classes are those of Storer (1966): 1 = 3.4–8 g, 2 = 8–15.6 g, 3 = 15.6–27 g, 4 = 27–42.9 g, 5 = 42.9–64 g, 6 = 64–91.1 g.

food consumption of nestling male and female Sparrowhawks and attributed the high food consumption of the smaller males to more rapid development than the larger females. It is unlikely that equal food consumption by the sexes persists for very long after fledging; we suspect that males soon consume less than females. Our Manitoulin Island brood consisted of 3 females and 1 male, the spruce-fir brood of Snyder and Wiley consisted of 2 males and 1 female (after the loss of 1 male), and the Puerto Rican brood consisted of 2 males. Assuming that the adults were responding to the needs of the young, the sex ratio of the broods thus relates rather well with changes in food deliveries after the fifth week. If we take the above factors into consideration, the temporal patterns of food deliveries to the 3 broods discussed above are basically similar.

In contrast, the riparian canyon brood of Snyder and Wiley showed a slight increase in food deliveries between week 5 and weeks 6 and 7 (the last 2 weeks were lumped because of limited observations). This high rate of food delivery at the end of fledgling dependency, and the considerable participation of the female in providing food, suggest that this brood

was suffering from food stress and that the parents were responding in accord with the hypotheses of Davies (1978) and Newton (1978). The riparian canyon nest was studied in 1971 during the worst drought in 50 years, and bird populations were judged to be low (Snyder and Wiley 1976). Our results show a precipitious drop in food deliveries early in the seventh week. It is possible that a similar, sudden decline occurred in most of the broods studied by Snyder and Wiley (1976) but was not recognized because of the very limited observations conducted during week 7.

Newton's (1978) hypothesis suggests that the relatively meager participation of the female in delivering food to the spruce-fir brood of Snyder and Wiley (1976) was due to adequate provisioning by the male. Snyder and Wiley suggest ". . . both sexes of adult accipiters hunt pretty much full time toward the end of the breeding cycle . . ." and suggest that the relatively low contributions of the female to the provisioning of the spruce-fir brood was due to her bringing relatively small prey. She also brought fewer prey items (11% of the total) than did the riparian canyon female (29% of the total). Snyder and Wiley attribute the difference in the feeding behaviors of the females at the 2 nests to a greater abundance of prey in the size range preferred by females in the riparian canyon habitat than in the spruce-fir habitat. We interpret the data in another way. A shortage in prey of the size classes preferred by the male in the riparian canyon habitat resulted in inadequate food deliveries by the male and increased participation by the female, while in the spruce-fir habitat, a reasonable abundance of prey in the size classes preferred by the male resulted in reasonable food deliveries by the male and the female was not induced to hunt regularly.

We feel that the data of Storer (Auk 83:423–436, 1966) offer the best estimate of prey-size preferences in sharp-shins. Storer examined the gut contents of 223 sharp-shins of which 82% were taken during migration, a period when one might reasonably expect random availability of the various size classes. The analysis of 249 prey items reveals that males prefer size classes 2 and 3 (73% of the total) and females prefer size classes 3, 4 and 2 (82% of the total). The preference of females for size class 4 is only very slightly greater than for size class 2 (Table 1).

An examination of Table 1 suggests that the male at the spruce-fir nest of Snyder and Wiley (1976) was taking larger prey than expected either in comparison to Storer's (1966) data or the prey available. The female took few prey, and it is not surprising that none were from the presumably few individuals available in larger size classes. The riparian canyon male took considerably smaller prey than the males of Storer (1966) or those of any other brood studied. We believe this is strong evidence of food stress. It appears that the male was doing the best he could during this "worst drought in 50 years," low bird populations and probably limited breeding by prey-birds. The riparian canyon female brought a larger proportion of the prey during the fledgling period than at any other nest: 53% (Manitoulin 37%, spruce-fir 22%, Puerto Rico 0%). In view of the high participation in feeding by the riparian canyon female, and the apparent scarcity of prey, the high proportion of large-sized prey taken is not surprising. It is possible that the male considerably depressed populations of smaller birds early during this unusually bad year. The limited data from the oak-juniper nest suggest that the male was preying on relatively large prey. The 4 prey items taken by the female are insufficient for comment. The Manitoulin Island male took larger prey than predicted on the basis of Storer's data and the same is true, to a lesser extent, for the female.

We believe that our intensive observations on Manitoulin Island, and our interpretation of the data of Snyder and Wiley, suggest that food stress late in the period of dependency of the young in Sharp-shinned Hawks is an exceptional phenomenon. We believe it occurred only in the riparian canyon brood of Snyder and Wiley (1976) during an unusually unfavorable year. We therefore conclude that food stress during breeding, ameliorated by separate feeding niches of the adults, is an unlikely explanation for the remarkable reversed dimorphism

in size exhibited by Sharp-shinned Hawks. It appears that, under most conditions, the female could contribute whatever prey is needed by the brood without having to be 1.7 times as large as the male and capturing slightly larger prey.

Acknowledgments.—We thank Mary Tasker for her exceptional hospitality to often unsociable field biologists and James Tasker for aid in the observations. J. A. Feduccia, K. D. Meyer and R. H. Wiley offered helpful comments on the manuscript. We thank T. J. Cade, R. T. Reynolds and N. F. R. Snyder for constructive criticisms of an earlier version of the manuscript; this does not mean that we have followed all of their suggestions or that they endorse our interpretations.—HELMUT C. MUELLER, *Dept. Zoology and Curriculum in Ecology, Univ. North Carolina, Chapel Hill, North Carolina 27514,* NANCY S. MUELLER, *Dept. Biology, North Carolina Central Univ., Durham, North Carolina 27707,* AND PATRICIA G. PARKER, *Dept. Zoology, Univ. North Carolina, Chapel Hill, North Carolina 27514.* *Accepted 10 Nov. 1979.*

Wilson Bull., 93(1), 1981, pp. 92–97

Food deprivation and temperature regulation in nestling Ferruginous Hawks.—Nestling deaths from heat prostration may occur regularly in some falconiform species (e.g., Fitch et al., Condor 48:207–237, 1946; Nelson, pp. 64–72 *in* Peregrine Falcon Populations, Their Biology and Decline, Hickey ed., Univ. Wisconsin Press, Madison, Wisconsin, 1969; Olendorff, U.S.I.B.P. Rep. No. 211, 1973; Beecham and Kochert, Wilson Bull. 87:506–513, 1975). Beecham and Kochert (1975) concluded that 41% of Golden Eagle (*Aquila chrysaetos*) nestling mortality in their Snake River, Idaho, study area was caused by overheating and observed that young birds in nests with a southern or western exposure are most vulnerable to heat stress.

The Ferruginous Hawk (*Buteo regalis*) nests in the semi-arid regions of southern Canada and the western United States (Olendorff 1973; Tomback and Murphy, unpubl.). Throughout the breeding range Ferruginous Hawks nest primarily on rocky outcrops, tops of trees (especially junipers [*Juniperus* spp.] and cottonwoods [*Populus* spp.]) and occasionally on sagebrush (*Artemisia* spp.) or the ground (Smith and Murphy, Brigham Young Univ. Sci. Bull. 18:1–76, 1973; Oldendorff 1973; Woffinden, Ph.D. diss., Brigham Young Univ., Provo, Utah, 1975; Howard and Wolfe, J. Range Manage. 29:33–37, 1976; Lokemoen and Duebbert, Condor 78:464–470, 1976; Fitzner et al., Condor 79:245–249, 1977). Despite the high temperatures encountered in the latter stages of the nesting cycle (e.g., Smith and Murphy 1973; Fitzner et al., 1977), apparently shade availability is not a nest-site requirement for the species. In the Great Basin west of Utah Lake, Woffinden (1975) examined 56 nests of Ferruginous Hawks on rocky outcrops, on the ground, and in trees. Almost half of these nests were unshaded throughout the day. The nests on steep slopes received some shade only in morning or afternoon, depending on slope aspect.

Here, we present field data suggesting that underfed Ferruginous Hawk nestlings are especially vulnerable to heat stress. We predict that combined effects of inadequate food provisions and high temperatures may cause much nestling mortality in years when prey populations are low.

On 15 June 1977, we surveyed Cedar and Rush valleys, Utah Co. and Tooele Co. (elev. 1760–1895 m; 40°00′N, between 111°55′W and 112°35′W), for Ferruginous Hawk nests (for detailed description of study area see Smith and Murphy 1973). Thirteen light phase nestlings between ca 5 and 7 weeks old remained in 5 nests, including 2 tree nests in Utah juniper (*Juniperus osteosperma*), 2 nests on rocky outcrops on steep (ca 40°), west-facing slopes, and

1 ground nest on a southeast-facing slope (ca 30°). Using a YSI Tele-Thermometer (Model 43E), a YSI black bulb probe and 2 YSI plastic-tipped probes, we measured ambient and cloacal temperatures of 2 nestlings 5.5–6 weeks old at a rocky outcrop nest from 14:00–17:00 on 24 June. A plastic-tipped probe was inserted 3–4 cm into the cloaca of each nestling, taped in place and checked each time the nestlings defecated. We erected a low cardboard barrier, non-reflective and brown in color, to prevent the young from leaving the nest. The nestlings showed no signs of agitation whenever we left our tent blind and approached the nest to take temperature readings.

On 23 June 1979, in the Raft River Valley, Box Elder Co., Utah, and Cassia Co., Idaho (elev. 1400–1700 m; 42°00′N, 113°30′W), we found 3 Ferruginous Hawk nestlings in 2 nests in Utah juniper (for description of study area see Howard and Wolfe 1976). One nest contained a melanistic bird, dubbed "Othello," ca 5 weeks old, and the second nest contained 2 light phase nestlings, "Iago" and "Desdemona," ca 5.5 and 6 weeks old, respectively.

Prior to the trip, we calibrated 3 miniaturized temperature-sensitive radio transmitters (Mini-Mitter Co., Inc., Model T). On 23 June, a transmitter was wrapped in Black-tailed Jackrabbit (*Lepus californicus*) meat and fed to each Ferruginous Hawk nestling, and the 3 birds were placed on a recently active Ferruginous Hawk ground nest which was unshaded throughout the day. We hobbled the young so they could not leave the nest to find shelter. Within 30 min the nestlings no longer struggled against the restraint and settled into position. We monitored transmitter signals from the nestlings 15 m from the nest by means of a Lafayette 3-Channel 1.5 Watt Receiver (Mini-Mitter Co., Inc., Model Ch receiver) and recorded ambient temperatures with a YSI black bulb probe and YSI Tele-Thermometer (Model 43TD). As indicated by signal strength, the transmitters lodged in the crops of the nestlings until they were regurgitated in pellets ca 24 h later. Transmitter signals were converted into body temperatures as follows: the receiver was switched to 1 of 3 channels and the time required for 100 clicks was recorded on a stopwatch. This time interval was compared to the appropriate calibration curve. Every 15 min from 13:30–17:00, we took body temperature readings and paired them with a black bulb ambient temperature reading.

The nestlings were transported in and maintained for 2 nights in individual grass-lined cardboard cartons. We fed them several times a day with fresh jackrabbit meat, hamburger and water. Cast transmitters were recalibrated and again fed to the birds. On 24 and 25 June 1979, we placed the nestlings on a recently active Ferruginous Hawk rocky outcrop nest built on a steep (ca 40°), west-facing slope in Cedar Valley, Utah Co., Utah. The nest was not shaded in the afternoon and the nestlings were again hobbled. On 24 June, we measured ambient and crop temperatures from 14:50–18:00. We did not feed the young on 25 June until 15:00 in the hopes of duplicating the effects of low food availability; black bulb ambient and crop temperatures were taken only from 12:00–14:00 to avoid the extreme late afternoon temperatures.

The behavior of the 5–7-week-old nestlings encountered in Cedar and Rush valleys in June of 1977 strongly suggested that ambient temperatures were uncomfortable, if not stressful. All of the nests were unshaded for half the day or longer. Three nestlings had wandered several meters from their ground nest and crouched under a small sagebrush (*Artemisia tridentata*). At 1 rock outcrop nest, the 2 nestlings had moved to the shade of a nearby man-made, small rock shelter. Two young hawks had moved 3–5 m from the other outcrop nest to lay their heads in the shade of a large rock. The 3 nestlings in each of the juniper nests were apparently unable to leave the trees. However, they all tended to pant rapidly and salivate. Angell (Living Bird 8:225–241, 1969) also reported "shade-seeking" behavior in nestling Ferruginous Hawks 4–4.5 weeks old. This thermoregulatory behavior is obviously an important means by which nestlings avoid overheating in the weeks prior to fledging.

In 1977, there were few active Ferruginous Hawk nests in the Cedar and Rush valley study

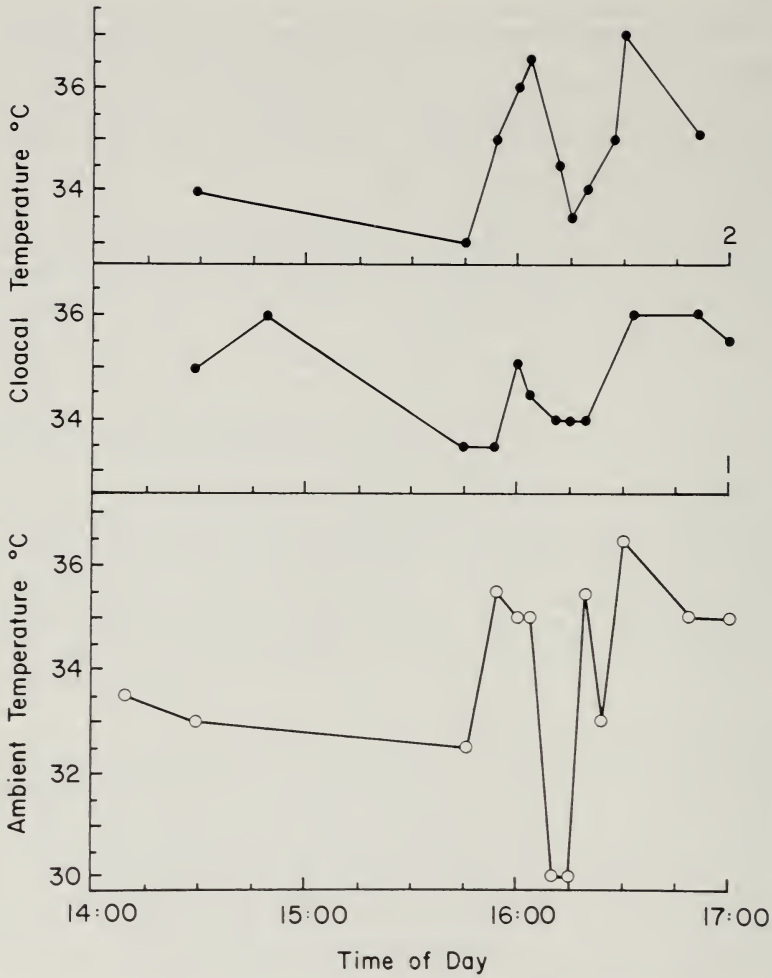


FIG. 1. Ambient temperatures and cloacal temperatures of 2 Ferruginous Hawk nestlings vs time of day at Cedar Valley nest, 24 June 1977.

areas (Murphy et al., unpubl.). The primary reason for the decline appeared to be a low population of Black-tailed Jackrabbits (Murphy et al., unpubl.). This jackrabbit is the principal food of the Ferruginous Hawk in the Great Basin region (Smith and Murphy 1973; Smith and Murphy, Raptor Research 13:1–14, 1979). Woffinden and Murphy (1977) showed a relationship between the annual numbers of Ferruginous Hawk nesting pairs and jackrabbit abundance. They also noted a high nestling mortality (an average of 49.5%) in 2 years of low jackrabbit density in 1973 and 1974.

In June 1977, we found no fresh jackrabbit remains at any of the nests we examined, although remnants of small prey items such as kangaroo rats (*Dipodomys* sp.), lizards (*Cnemidophorus* sp., *Phrynosoma* sp.) and birds (Icteridae) occurred at 2 nests. One or both

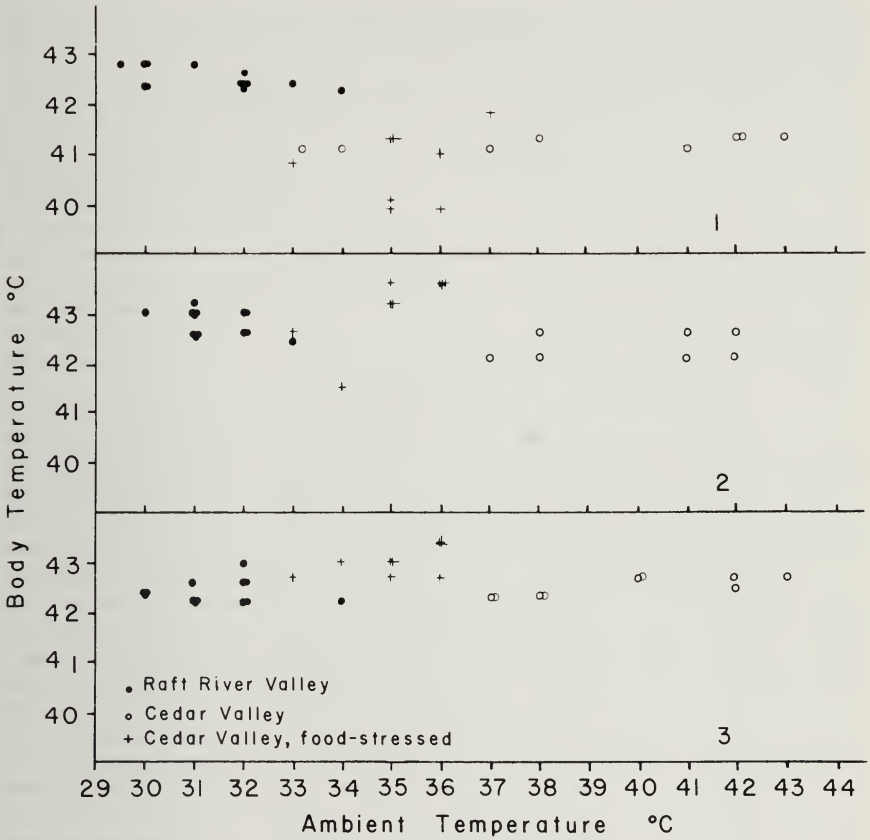


FIG. 2. Crop temperatures monitored by telemetry vs ambient temperatures for Ferruginous Hawk nestlings Iago (1), Desdemona (2) and Othello (3), June 1979.

parent birds circled overhead at all the nests we visited, indicating that the young were still attended.

At the rock outcrop nest where we took temperature readings, no fresh food was present during the 3 days of our visits. At all nests it appeared that young were inadequately provisioned during a time when food consumption rates should be maximal (Olendorff, Condor 76:766–768, 1974). A graph of black bulb ambient vs cloacal temperatures for the afternoon of 24 June (Fig. 1) suggests the nestlings had difficulty thermoregulating. The sky was partly overcast that day, and when the sun was exposed, black bulb temperatures at the nest increased rapidly from 30°–36.5°C. Nestling cloacal temperatures (range 33–37°C) increased and decreased rapidly with ambient temperature. These body temperatures are lower than those daytime temperatures reported for other falconiforms (e.g., McNab, Condor 68:47–55, 1966; Fitch, Condor 76:331–333, 1974; Rudeen and Powers, Condor 80:447–449, 1978), possibly a consequence of both the cloacal temperature (rather than deep core temperature measurement) and an impaired thermoregulatory capacity. Both nestlings began panting

continuously each time their temperatures reached 35°C. Fluctuations in body temperature of nestling #2 were more extreme than those of #1 (F-test NS); nestling #2 was not found during our last visit on 25 June.

The 3 nestlings from Raft River Valley in 1979 were seemingly well-fed prior to our experiments, judging by the fresh jackrabbit remains. Body temperatures of the 3 nestlings monitored by telemetry ranged from 39.9–43.6°C (Fig. 2), and black bulb ambient temperatures ranged from 29.5–43°C. These body temperatures are higher than those of the 1977 Cedar Valley nestlings and indicate either that there is a difference between temperatures measured in cloaca and crop, that the 1977 nestlings were suffering from starvation and could not thermoregulate well, and/or that the 1979 Raft River Valley nestlings were stressed by heat and restricted movement on the nest. This latter possibility is unlikely, since we obtained similar crop temperatures for the Raft River Valley nestlings in a resting state in the laboratory (Tomback and Murphy, unpubl.). However, the 3 initial 23 June 1979 readings of 42.7°C for Iago and 1 initial reading of 43.2°C for Desdemona at the Raft River Valley nest (Fig. 2) may have been elevated by our handling.

Means and standard deviations (°C) for ambient and nestling body (crop) temperatures for the 3, 1979 experimental periods are as follows: Raft River Valley, 23 June—T_A 31.4 ± 1.06, Iago 42.5 ± 0.21, Desdemona 42.8 ± 0.25, Othello 42.4 ± 0.24; Cedar Valley, 24 June—T_A 39.4 ± 2.74, Iago 41.2 ± 0.11, Desdemona 42.3 ± 0.27, Othello 42.5 ± 0.20; and Cedar Valley, 25 June—T_A 35.1 ± 1.06, Iago 40.7 ± 0.72, Desdemona 43.1 ± 0.74, Othello 43.0 ± 0.29. F-tests indicated that ambient temperature varied more on 24 June than on either 23 June ($P \leq 0.01$) or 25 June ($P \leq 0.01$). Yet, the crop temperatures of both Iago and Desdemona fluctuated most extremely on 25 June, when the nestlings were deprived of food, than on either 23 June ($P = 0.01$, both nestlings) or 24 June ($P = 0.01$, $P = 0.05$, respectively). The crop temperatures of Iago varied more on 23 June than 24 June ($P = 0.05$), whereas those of Desdemona varied much the same. For Othello crop temperature varied similarly on all 3 days. However, the crop temperatures measured for both Othello and Desdemona under conditions of food deprivation were significantly higher than those temperatures monitored on either 23 or 24 June (Mann-Whitney *U*-test, $P \leq 0.001$), even though the ambient temperatures of 25 June were lower than those of 24 June. Body temperatures for Iago were lower on 25 June than on previous days (Mann-Whitney *U*-test, $P \leq 0.001$), even though they fluctuated more. Iago rarely panted on 24 June, while the other nestlings panted most of the time and occasionally held their wings out to the sides to facilitate cooling. The high temperatures on 24 June affected Othello most severely, as the panting and posturing of this nestling were pronounced and almost continuous. It is possible that Othello's dark plumage increased his heat burden (Hamilton and Hepner, Science 155:196–197, 1967; Lustick, Science 163:387–390, 1969; but see Wahlsberg et al., J. Comp. Physiol. 126:211–222, 1978).

In conclusion, the temperature fluctuations of the underfed nestlings at the Cedar Valley nest in 1977 and the significantly higher and more varied body temperatures of the underfed nestlings in 1979 suggest that food deprived nestling Ferruginous Hawks cannot cope with heat stress. Reduction in prey probability are known to result in high nestling mortality in the Ferruginous Hawk (Woffinden and Murphy 1977). Heat prostration may be a major cause of nestling deaths under such conditions, especially since Ferruginous Hawk breeding grounds are characterized by high summer temperatures and nests are unshaded for all or part of the day.

Acknowledgments.—We thank Dan Johnson, Kent Keller and Philip Murphy for their invaluable help in the field and Clayton White for Raft River Valley nest information. Fieldwork in 1977 was funded in part by a grant from the Chapman Memorial Fund of the American Museum. At that time D. F. Tomback held a postdoctoral fellowship from Brigham Young University. Data and manuscript preparation by D. F. Tomback was supported by the De-

partment of Biology, University of California at Riverside. Keith L. Bildstein, a reviewer, provided helpful suggestions concerning the manuscript.—Diana F. Tomback, *Dept. Zoology and Entomology, Colorado State Univ., Fort Collins, Colorado 80523,* and Joseph R. Murphy, *Dept. Zoology, Brigham Young Univ., Provo, Utah 84602. Accepted 10 Jan. 1980.*

Wilson Bull., 93(1), 1981, p. 97

Aerial "play" of Black Vultures.—Occasionally I have seen Black Vultures (*Coragyps atratus*) engage in playlike, aerial acrobatics at Cerro Verde (13°50′N, 89°38′W; 2000 m elev.), El Salvador. On 15 November 1971, I was present during a violent "Norte," a prolonged windstorm which may attain gale velocity on mountain tops. I noticed, without heeding at first, sounds I attributed to a child tooting a musical toy. Then a trio of Black Vultures shrilled past my head, producing a sound like that of an aeolian harp, caused undoubtedly by wind passing through the feathers of wings and/or tails.

A dozen or more Black Vultures were soaring in the strong upslope winds on the north side of Cerro Verde, being carried upwards as much as 500 m above the summit. From time to time one or more birds "peeled off" to dive precipitiously towards the southeast, the wind behind them. Some leveled off where I could see them; others continued out of sight, descending more than 700 m. Recordings of their sounds, made at the time, suggest diving wire-strutted biplanes of the First World War.

One trio was especially notable, diving again and again as a team. I watched them make some 25 dives, 3 of which ended near me. The birds dove sometimes in V-formation, sometimes in line and attained impressive speeds. They ended the dives in 2 steps: (1) a slight increase in angle of attack which checked their speed slightly and flattened the dive; and (2) a sharp increase in attack angle plus spreading and lowering the tail which forced them into a shallow climb. They then used their forward momentum to circle along the lee side of the mountain into the upward current again. The leader of a dive also led in the following ascent but I could not ascertain whether it retained that position in subsequent dives.

I have heard since, under less favorable conditions, the shrill of diving Black Vultures during strong Nortes. I add only that twice I saw single vultures diving as described above. I noted that a single bird produces several tones, suggesting that several feathers are involved.

Bent (U.S. Natl. Mus. Bull. 167:29, 1938) described similar diving sounds produced by courting Black Vultures. Brown and Amadon (Eagles, Hawks and Falcons of the World, McGraw-Hill, New York, New York, 1968:181) reported sounds like ripping heavy paper as Black Vultures dive for food. The birds at Cerro Verde were not diving for food and did not seem to be courting. Brown and Amadon (1968:101) refer to certain otherwise unclassified aerial maneuvers of falconiformes as communal displays. However, a display implies communication between a sender and an intended observer; this does not apply to lone birds. I have no notion of the incentive which governed the vultures I watched, but to me the exuberant quality of their behavior, so unlike our usual impression of the species, had "all the appearances of play and seemed to serve no other function than the release of pent-up energy" (Pettingill, Ornithology in Laboratory and Field, Burgess Publ. Co., Minneapolis, Minnesota, 1970:254).—Walter A. Thurber, *Cornell Univ. Laboratory of Ornithology, 159 Sapsucker Woods Road, Ithaca, New York 14853. Accepted 30 Nov. 1979.*

Wilson Bull., 93(1), 1981, pp. 98–99

The shoulder-spot display in Ruffed Grouse.—Although the "shoulder-spot" display is widespread in Tetraonidae, Lumsden (Living Bird 9:65–74, 1970) and Hjorth (Viltrevy 7:184–596, 1970) were both unable to find evidence of this display in Ruffed Grouse (*Bonasa umbellus*). The shoulder-spot display is most frequently seen in ambivalent (also termed conflict by Lumsden 1970) situations containing strong elements of fear. The behavior patterns associated with fear are difficult to observe in wild Ruffed Grouse because of the general wariness of the species and the restricted visibility characteristic of Ruffed Grouse habitat. These observational difficulties may have resulted in this behavior being overlooked when Ruffed Grouse were observed in a natural setting.

A colony of captive Ruffed Grouse at the University of Guelph, Guelph, Ontario, provided

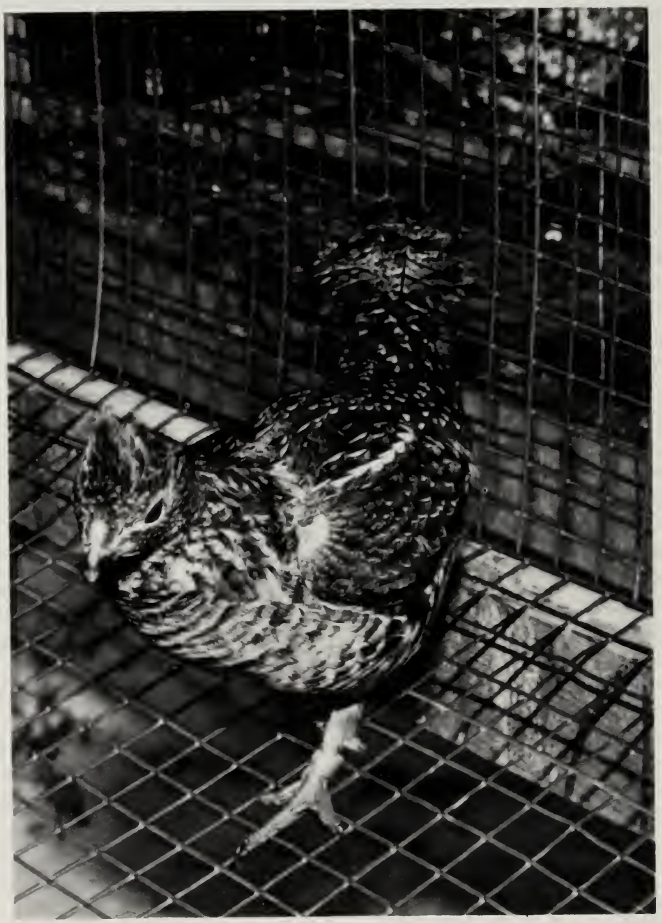


FIG. 1. A male Ruffed Grouse displaying a shoulder spot.

the opportunity for extended observations of grouse behavior. The shoulder-spot display was observed in many males on numerous occasions. By contrast, no females were observed using this display.

Copulation is the activity during which the shoulder-spot display has been most frequently seen in females of other grouse species (Lumsden 1970). However, our captive females rarely permit normal copulation, and the observation of copulation is very rare in captivity. Therefore, failure to observe the shoulder-spot display in female Ruffed Grouse may be attributable to the rarity of copulation by captive hens rather than to the absence of this display in female Ruffed Grouse.

The shoulder-spot display was most frequently observed in captive males performing what has been termed the "intimidation" display (Aubin, M.Sc. thesis, Univ. Alberta, Edmonton, Alberta, 1970) or "upright-cum-ruff" (Hjorth 1970) display. When a male performing the intimidation display is approached by an observer, the male usually attacks or retreats within a short time. However, some males are reluctant to do either, leading to an ambivalent situation. If the ambivalence is sufficiently intense, the male assumes a semi-upright posture, with all feathers except the crest sleeked. In this posture, he alternately approaches and retreats from an intruder, with his body held at a slight angle to the intruder. He may threaten to strike with his bill. Before this strike intention movement is made, the wings are withdrawn from beneath the contour feathers, and are slightly extended. The shoulder-spot display is performed just before the wings are extended (Fig. 1).

Close examination of birds performing this display revealed that the shoulder-spot is formed by exposure of the underwing coverts on the upper surface of the wing, as Lumsden (1970) thought. From examination and manipulation of the wings of live birds, it does not seem possible that a simple re-alignment of the underwing coverts could produce a shoulder-spot of the dimensions seen on many males. The exposure seems to be effected by movement of the patagial skin, accompanied by repositioning of the feathers. Apparently, the skin is drawn over the leading edge of the wing, and onto the upper surface. The coverts are then exposed to form the shoulder-spot. By varying the degree of skin movement and feather rearrangement, it would be possible for the bird to alter the dimensions of the shoulder-spot displayed.

Similarities between Ruffed Grouse and other grouse species in the method of effecting this display, and the context within which it is performed indicate the origin of the shoulder-spot display is similar in all grouse. These observations support the suggested evolutionary development, whereby the display is derived from what was originally a flight intention movement (Hjorth 1970, Lumsden 1970).

Financial support for the maintenance of the grouse colony was provided by the Ontario Ministry of Natural Resources and the University of Guelph.—Allan Garbutt, *Dept. Zoology, Univ. Guelph, Guelph, Ontario N1G 2W1 Canada.* (Present address: *1424 Carlyle Rd., Calgary, Alberta T2V 2V1 Canada.*) *Accepted 3 Feb. 1980.*

Wilson Bull., 93(1), 1981, pp. 99–103

The agonistic repertoire of Sandhill Cranes.—Detailed descriptions of agonistic displays are lacking for wild Sandhill Cranes (*Grus canadensis*). Walkinshaw reports that all cranes have some of the same aggressive displays (Walkinshaw, Cranes of the World, Winchester Press, New York, New York, 1973). Masatomi and Kitagawa (J. Fac. Sci., Hokkaido Univ., Ser. IV, Zool. 19:834–878, 1975) give a thorough description of agonistic behavior in the Japanese Cranes (*G. japonensis*) that facilitates description of such behavior in Sandhill Cranes. Voss (pp. 63–85 *in* Eastern Greater Sandhill Crane Symposium, R. D. Feldt, com-

piler, Michigan City, Indiana, 1977) describes agonistic behavior in captive and wild Greater Sandhill Cranes (*G. c. tabida*) on the summer range in Wisconsin. Here we present observations of agonistic behavior of migratory Greater Sandhill Cranes on their winter range in Florida and summer range in Wisconsin and year-round observations of the resident Florida Sandhill Crane (*G. c. pratensis*) based on approximately 700 h of fieldwork at Paynes Prairie, Alachua Co., Florida and at the International Crane Foundation, Baraboo, Wisconsin. We also include the contexts under which these agonistic behaviors were given. Approximately 80% of the birds observed in Florida had been captured (Nesbitt, pp. 299–303 *in* Proceeding of the International Crane Workshop, J. C. Lewis, ed., Oklahoma State Univ., Stillwater, Oklahoma, 1975), individually color marked and their sex and approximate age determined. Sex was determined by laporatomy or from postures assumed during Unison Calling, a sexually distinct display. Age was determined from plumage characteristics.

Highly dominant displays are given by individuals that have little or no fear of other cranes. If 2 highly aggressive cranes confront each other Bill Sparring usually results. This display begins when the 2 birds approach each other, some preliminary bill jabbing ensues, then with wings extended, neck feathers erect and bill tips close together (Fig. 1A), the birds vocalize and vault into the air throwing feet and wings forward (Fig. 1B). Substantial contact does not usually occur, but there is a risk of injury from feet or bill. In many instances, this display is very brief, lasting only 2 or 3 sec and does not progress beyond the initial bill jabbing. The victor stands his ground while the loser retreats giving any of the 6 escape postures described by Masatomi and Kitagawa (1975). Archibald reported a similar display in the Hooded (*Grus monacha*) (Animal Kingdom 77:19–24, 1974) and White-naped (*Grus vipio*) cranes (Animal Kingdom 76:17–21, 1973) as does Walkinshaw (1973) for Sandhills. Bill Sparring probably is important to the establishment of a dominance hierarchy. Kepler (pp. 177–196 *in* Proceeding of the International Crane Workshop, J. C. Lewis, ed., 1975) discusses the occurrence of a linear dominance hierarchy in a flock of 9 captive-reared Whooping Cranes (*G. americana*). A similar hierarchical system was noticed in the wild among adult male Sandhill Cranes and may exist through other social groups of sandhills as well. During another high intensity agonistic display, the Head Lowered Charge (Fig. 1D), the aggressor rushed quickly at another bird, neck extended, head, neck and body held horizontal, wings usually tight to the body. Sometimes flapping begins as the other bird is approached, the bill is open, and the aggressor often grabs the other bird by the wing or scapular feathers. A charge can occur during feeding where the aggressor, apparently feeding normally, moves closer to the offending individual. Then from the feeding position a charge erupts catching the other crane by surprise. Walkinshaw (1973) has generally described this behavior as occurring with all cranes. The Head Lowered Charge often leads to Aerial Pursuit, especially during the period when the birds are defending nesting territories. During Aerial Pursuits the aggressor may attempt to strike the fleeing bird with its feet. A dominant crane will displace a subordinate individual from a feeding or drinking site with a Bill Stab (Fig. 1E) directed at the back or back of the neck with bill either open or closed. The attacked bird simply moves a few steps, and the dominant bird assumes the feeding or drinking spot. Charges or stabs from the dominant individual often follow a full Bill Sparring episode. Following all high intensity agonistic displays, the dominating individual usually gives a Low Bow display (Masatomi and Kitagawa 1975, Voss 1977) during which the neck is arched and the head slowly lowered toward the ground displaying an expanded bright red comb. The display terminates with the head between the bird's legs and bill held vertically (Fig. 1F). As the head is lowered the bird emits a low growl. A Low Bow is often given by territorial birds upon landing near an intruder before any other signs of aggression are shown.

During agonistic episodes where the motivation levels are lower, any one of a series of generalized ambivalent displays may be seen. To drive other cranes from a defended territory

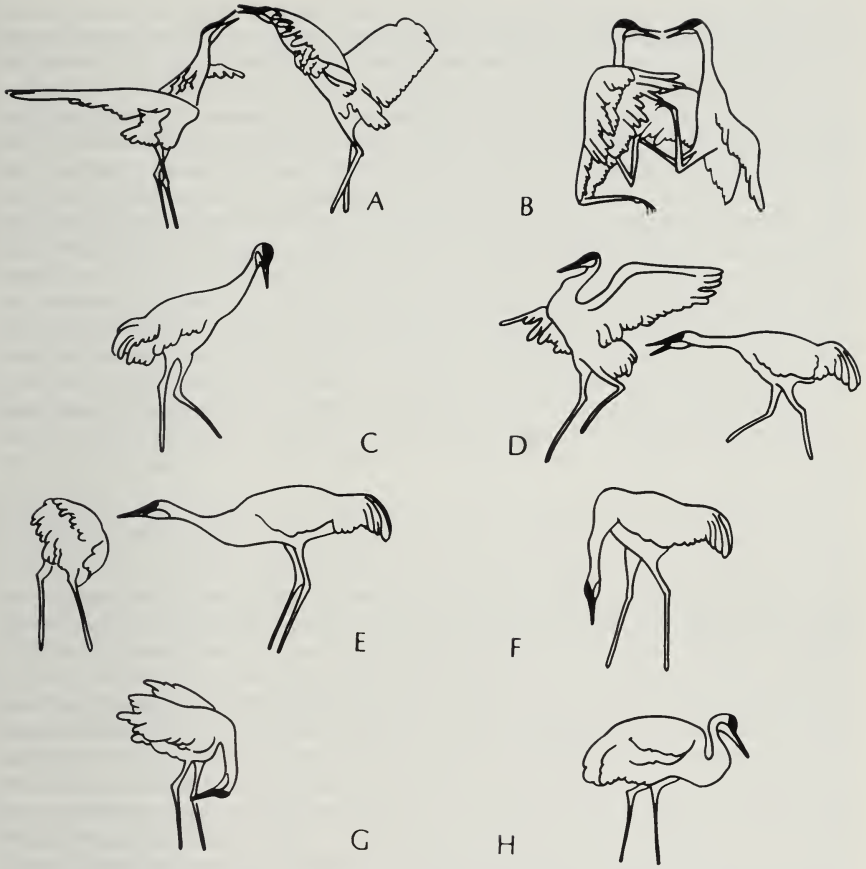


FIG. 1. Common agonistic displays of Sandhill Cranes: (A, B) Bill Sparring; (C) Directed Walk Threat; (D) Head Lowered Charge; (E) Bill Stab; (F) Low Bow; (G) Generalized Body-Wing Shaking; (H) Neck Retracted Submissive Posture.

or a feeding area, the dominant individual or pair (and their chick, if present) give a Directed Walk Threat or Adornment Walking (Masatomi and Kitagawa 1975, Voss 1977) often with a characteristic vocalization (Slow-rattle Family Call; Nesbitt and Bradley, in press) given in unison, by all defending cranes. This display is an exaggeration of the normal upright walking movement directed at a particular individual. The displaying bird circles the opponent with a stiff gait characterized by animated head pumping and tertials slightly raised. With each step the neck is extended and the bill pointed at the other crane. Periodically, the bill is angled downward displaying an expanded, bright red comb (Fig. 1C). The Directed Walk Threat is apparently equivalent to a display described by Archibald (1974) for the Hooded Crane. The individual toward which this behavior has been addressed usually moves away quickly with head lowered and body held horizontally. Other adornment displays described by Masatomi and Kitagawa (1975) for *G. japonensis* seem to represent variations in

the intensity of adornment walking in sandhills. If the offending individual does not retreat as a result of the Directed Walk Threat a charge or stab may occur. If the aggression level is not high, one of several ritualized general threat displays may ensue. The Generalized Body-Wing Shaking (Voss 1977) (Fig. 1G), similar to the Low Bow, has been described for several species of cranes (Archibald 1974; Walkinshaw 1973; Paulsen, Dansk Ornithol. Forenings Tidsskr. 69:119–122, 1975). But it is less intense and general rather than directed. Body-Wing Shaking begins as a stylized feather maintenance movement, contains a less dramatic bow and terminates with displacement preening of the legs or belly. Again a low growl is given as the head is lowered. In Sandhill Cranes other forms of bowing described by Masatomi and Kitagawa (1975) appear to be less intense versions of the Low Bow. The Unison Call may function as a generalized aggressive display (Archibald, Ph.D. diss., Cornell Univ., Ithaca, New York, 1976). A pair will often Unison Call before aggressive episodes or after successfully driving intruders from a defended territory. The Crouch Display observed by Voss (1977) principally in young cranes was noticed among the Florida birds only once, given by a young crane. In the wild it is perhaps a seldom given display that in adult birds transmits little or no agonistic information. When 2 cranes with lower aggressive motivation are close together, they often engage in displacement foraging or preening. These are transitional behaviors leading to normal feeding or preening and away from aggressive encounters.

In fearful situations, birds of the year and other subordinant individuals wishing to avoid attack, assume a Neck-retracted Submissive Posture (Voss 1977) (Fig. 1H), during which the comb is constricted and dull in color. A crane, fearful of attack from another crane, may feign the precopulatory display with wings spread and beak held above horizontal at a 45° angle, thus changing the motivation of the attacker. When approached by a mammalian predator, Sandhill Cranes give a predator threatening Spread-Wing Display (Voss 1977), consisting of an upright posture with wings held high and half-open. The head is held high with the beak pointed directly at the predator. If the predator does not retreat, then the bird approaches, thrusts the bill forward and hisses. A crane was observed successfully fending off the attack of a juvenile Bald Eagle (*Haliaeetus leucocephalus*) using bill jabs with vaults and forward thrusting of the feet and wings. Such movements, similar to Chasing and Kicking (Voss 1977), are generally equivalent to the movements that have been stylized into Bill Sparring, but without the characteristic vocalizations. A similar attack behavior and hissing has been observed during trapping operations when oral tranquilizers were used. Attacks were directed at tranquilized cranes that did not react normally to unaffected birds. Presumably this is the type of attack that has resulted in severe injuries to cranes (Walkinshaw, Michigan Acad. Sci., Arts, Letters 40:75–88, 1965). The attack method described by Altmann (J. Mammal. 41:525, 1960) employed by a pair of adult cranes with a chick to drive off a moose (*Alces alces*) incorporated these same movements.

Aggression was often observed during and after unpaired dancing bouts between nonbreeding cranes. Aggressive attacks were also launched at individuals apparently preoccupied in another behavior such as Bill-Raising (Masatomi and Kitagawa, 1975:Fig. 119), unilateral stretching or sitting.

All of these displays have been observed in both sexes, though Bill Sparring appears more pronounced in males. Sub-adult cranes exhibited the same aggressive displays, but the frequency and intensity of the displays were much reduced when compared with paired males. Among 4 of 5 distinctly marked breeding pairs the male consistently took the leading role in territorial defense. Within the fifth pair, the male and female were equally aggressive, both initiating an equal number of encounters. Females and young of the year commonly participate in Directed Walk Threats, and occasionally Charges. Other displays appear much less frequently. The hierarchical position of the pair or family seems to depend on the

position of the male. The aggressiveness and therefore the hierarchical position of a male relates to the presence of a chick. Pairs without chicks tend to be lower in the order. For example, the dominant pair of the 5 marked pairs had 1 chick in 1977. In 1978, they were chickless and were dominated by 2 previously subordinate pairs, both with chicks.

The frequency of agonistic encounters involving adult Florida cranes increased during the period when young of the previous year were separated from the family group (February and March). The frequency remained high until just before the eggs hatched, then the level declined and the number of encounters remained low until several weeks after hatching. This lowered aggression period corresponds with the period in which Bennett (Auk 95:411–413, 1978) noticed little response from territorial cranes to the play back of tape recorded calls.

We wish to thank K. S. Voss and C. B. Brownsmith for their comments on early drafts of this manuscript. This study was in part a contribution of the Federal Aid to the Wildlife Restoration Program, Florida Pittman-Robertson Project W-41.—Stephen A. Nesbitt, *Florida Game and Fresh Water Fish Commission, Wildlife Research Laboratory, 4005 S Main St., Gainesville, Florida 32601* and George W. Archibald, *International Crane Foundation, Baraboo, Wisconsin 53913.* *Accepted 1 Nov. 1979.*

Wilson Bull., 93(1), 1981, pp. 103–107

Notes on the Slender Antbird.—The Slender Antbird (*Rhopornis ardesiaca*), first collected somewhere in eastern Brazil by Prince Maximilian von Wied (Beiträge zur Naturgeschichte von Brasilien, Vol. 3, 1831), was until recently known from 3 specimens: the male type, another male from Ituaçú, in south-central Bahia, and a female from the town of Boa Nova just down the Rio de Contas (Naumberg, Bull. Am. Mus. Nat. Hist. 76:231–276, 1939). Emil Kaempfer collected the last 2 specimens in 1928. Naumberg suggested that Kaempfer's "Boa Nova" was another town with the same name, northwest across the Rio São Francisco; but Kaempfer was at the second Boa Nova in 1927, not 1928. Moreover, Wied is likely to have collected the type near the first Boa Nova, which he passed en route from Vitória da Conquista to Salvador.

From 3–9 December 1974, we studied Slender Antbirds in patches of dry forest on Fazenda Alvorada, just north of the first Boa Nova (14°20′S, 40°11′W). A good, if scattered, population exists in these patches, which are gradually being cleared for cattle pastures. In 1977, H. Sick collected a male at Boa Nova after we mentioned our observations to him.

Habitat and foraging.—Boa Nova lies at 700 m elev., below 800–1000 m ridges of the northern end of a broad plateau that stretches southwest past Vitória da Conquista nearly to the valley of the Rio Pardo in the state of Minas Gerais (Fig. 1). This plateau is the main ridge of southeastern Bahia, forming a border between wet coastal forests (which include some patches of dry forest in the upper basins of small rivers) and the desert scrub or "caatinga" of the interior.

The natural vegetation of this rolling plateau varied within short distances from wet cloud forests (1500–2000 mm annual rainfall) on the eastern escarpments to caatinga in such rain-shadow areas as the lee slopes around Boa Nova, but the summit was mainly a dry forest (800–1000 mm rainfall) with many "cipós" or lianas—a "mata de cipó." The scattered remaining patches of dry forest have a strange appearance, with scattered white trunks of small trees above a dense layer of midstory trees and vines. The understory is fairly open, but blocked here and there by lianas and by patches of huge terrestrial bromeliads (*Aechmea* sp.). In the forest, bromeliads tend to sit high on tree trunks; but at the borders between dry

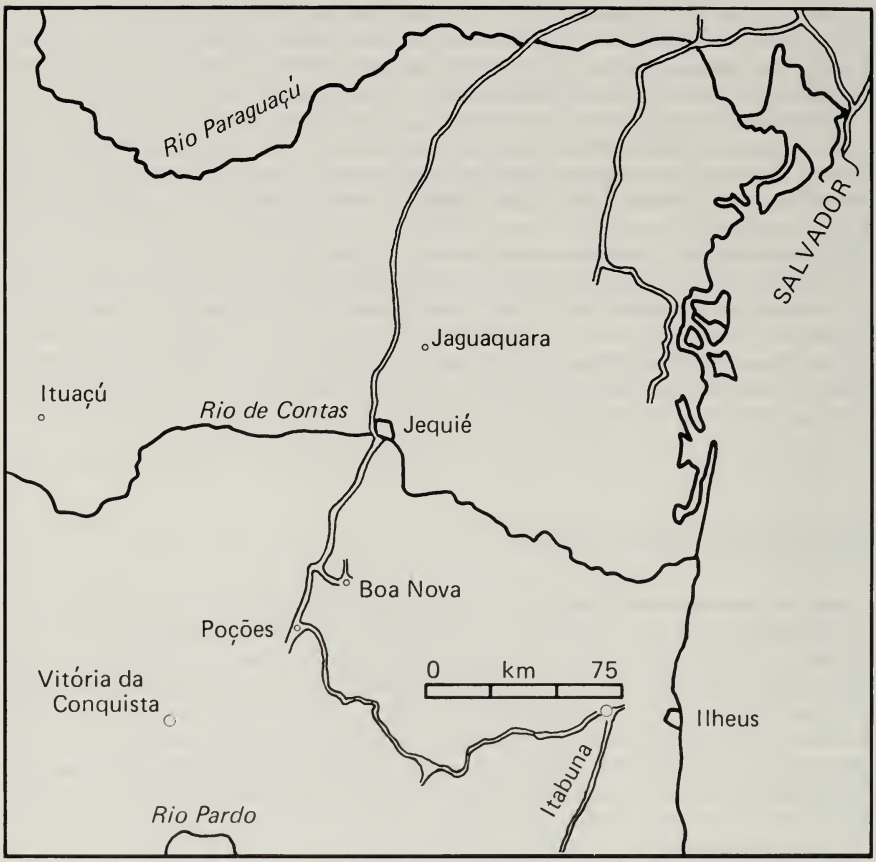


FIG. 1. Coastal Bahia, Brazil, showing the region inhabited by Slender Antbirds. The only roads shown are ones traveled by the authors.

forest and caatinga, or between dry forest and pastures, there is enough light for the bromeliads to descend to the ground. These bromeliads, and surrounding undergrowth near the forest edge, are the habitat of Slender Antbirds.

Just inside the forest borders—occasionally in tall scrub nearby—the antbirds hop on the ground, low vines and on the tops of bromeliad leaves, pausing now and then to swipe dead leaves from atop the bromeliads or from spots on the ground. They wander silently much of the time, peering up and down and capturing small grasshoppers or other insects by short flights or by hopping down to peck. We found them surprisingly like Gray Catbirds (*Dumetella carolinensis*) of North America in their appearance and actions, although they stay on the ground much more.

Members of a pair wander separately or together, often disappearing among the dense bromeliads for 15 min or more, only to reappear less than 5 m from where they entered. Each pair we watched seemed to have a very limited home range, barely 50 m across; but home ranges of pairs were usually separated by 100 m or more because patches of bromeliads

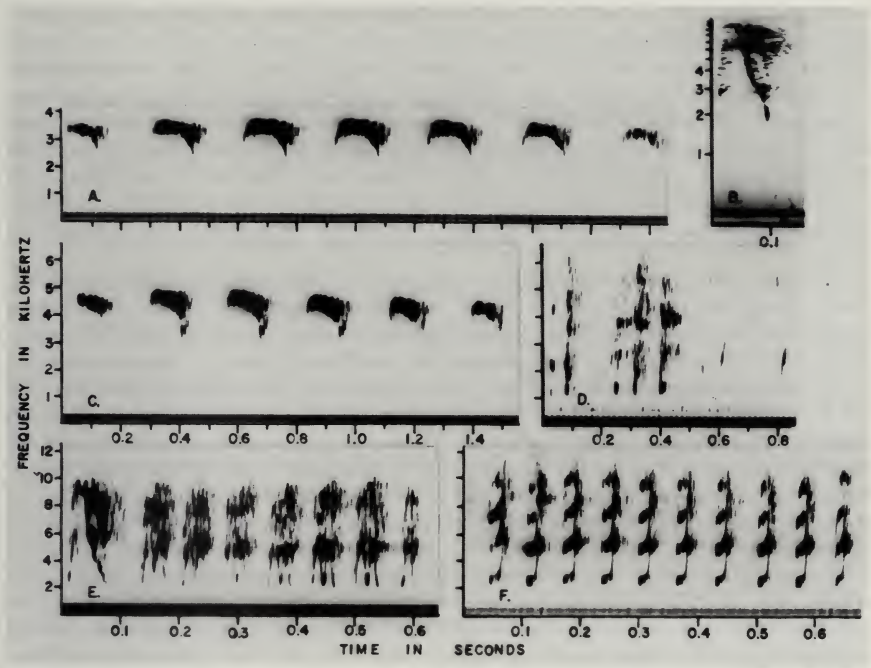


FIG. 2. Audiospectrographs of Slender Antbird vocalizations: (A) song of male; (B) alarm chip (logarithmic scale); (C) song of female; (D) faint chirps and grunts of a pair; (E) rattle, starting with a chip; (F) rattle of another bird.

were seldom close together. Occasionally we found birds hopping on the ground through fairly open undergrowth between patches of bromeliads, and once 2 such pairs were singing as they hopped along a presumed territorial boundary. In the center of the main forest tract of Fazenda Alvorada, we encountered only 1 bird near a bromeliad zone in a treefall clearing. Maximum densities were in a rather scrubby second-growth woodlot, where pairs were 100–200 m apart.

We found no *Rhopornis* following army ants within the main woodlot; there the related White-winged Fire-Eyes (*Pyriglena leucoptera*) and White-bibbed Antbirds (*Myrmeciza loricata*) split the niche of the Slender Antbird. Its niche is essentially that of another slender and long-legged forest-edge antbird, the White-bellied Antbird (*M. longipes*), a species that follows army ants occasionally in Panama, Trinidad and other areas.

Song and vocal behavior.—The simple and loud *peer peer peer peer peer peer* song of Slender Antbirds (Fig. 2A, C) is audible up to 500 m from the forest edge, and seems well adapted for birds that live widely scattered along forest edges in isolated patches of dense cover. Songs began 15–60 min after the first light and after the first songs of other diurnal birds, hence between 05:20 and 06:00. Sessions of song were irregular, mostly during the morning; few birds sang at any time. Songs were rare after 13:00 or 14:00. Often the male started singing when the female disappeared, she would finally answer him a few times, and the two would move together again. One male sang off-and-on for nearly 2 h (05:40–07:30)

until the female appeared. At times, 2 males or 2 pairs sang back and forth for short periods, mostly in boundary disputes.

When the pair met and foraged close together, they exchanged faint *sif* or *prit* and other notes (Fig. 2D), some rather like the "bubbling" call of White-backed Fire-Eyes. The male occasionally started a "serpentine-song" of the type common in antbirds: an alternating series of slow and fast chirps, *eu, eu, u-u-u-u-u, eu, eu, eu, eu* . . . and so on. One male fed his mate a small grasshopper after serpentine-singing. Another pair carried small insects to a patch of bromeliads and rattled repeatedly at the observer; but on other days the female rattled only near another patch of bromeliads. Otherwise there was no evidence of breeding activity.

Individual birds varied widely in their reactions to us. Some foraged quietly and tamely, others quickly fled to dense vegetation and others scolded vigorously. None was as difficult to observe as are antbirds of the rain forest, perhaps because Slender Antbirds live next to good cover rather than in open undergrowth. The usual alarm calls are a sharp chipping and a loud rattling. Chipping is a loud sibilant *tsiek*! or *psief*! (Fig. 2B) as the bird pounds the tail downward before or after fleeing to cover. At times the call becomes a loud *feeyou*! or *phew*!, perhaps a different note. An approaching or mobbing bird opens the beak widely and rattles loudly, *wi-i-i-i-i-dit*! (Fig. 2E, F). The song and all these alarm calls are like calls of Black-headed Antbirds (*Percnostola rufifrons*), but also resemble calls of antbirds of the genera *Myrmeciza* and *Pyriglena*. The song and rattle are especially like those of all the species of *Pyriglena*, and can be confused with notes of *Pyriglena leucoptera* at Boa Nova. The songs of Narrow-billed Antbirds (*Formicivora iheringi*), common in lower midlevels of dry forest at Boa Nova, are like slow and faint versions of the songs of Slender Antbirds. Competitive mimicry (Cody, Ann. Rev. Ecol. Syst. 4:189–211, 1973) in voice seems possible, although the 3 species do not overlap much in foraging.

Conservation.—Dry forest in central southern Bahia is rapidly being cleared for cattle, according to CEPLAC, the Cocoa Institute at Itabuna and Renato Aragao, former director of the Institute Brasileiro de Desenvolvimento Florestal at Salvador. The initial stages of clearing for cattle, creating many zones of forest edge, probably benefit Slender Antbirds. However, patches of forest are decreasing in size and length of edge. At Fazenda Alvorada, cutting a corner of the woodlot near the ranch houses to plant corn and beans had trapped 1 pair of Slender Antbirds in a patch 50 × 100 m. Early each morning they hopped out through newly felled trees, searched a bit and gave alarm notes, and soon returned to bromeliads in the decreasing bit of forest. Another edge of the main woods was recently cleared to plant introduced grass, even though wide areas of pasture nearby were reverting to scrub. On the far side of the main woodlot, a neighbor was also clearing new areas. One can see cleared slopes all around Boa Nova, so the fate of Slender Antbirds is certainly in doubt. The pattern in similar areas in São Paulo state has been to clear all forests, then plant eucalyptus or pine for crops when hills start to erode and pastures are no longer worth weeding.

Slender Antbirds should be kept on the Endangered or Vulnerable lists of the International Council for Bird Preservation. Another species restricted to mata-de-cipó, *Formicivora iheringi*, should probably be added to the list. A forest reserve of mata-de-cipó is certainly desirable, just as it would be good to have reserves in all distinctive types of vegetation, or even better to preserve a natural framework of vegetation in all regions. One idea for Boa Nova would be a reserve in conjunction with an agricultural experiment station, which is needed on the plateau because of its distinctive climate, soils, etc. The problem remains that species often disappear from reserves (Willis, Ecol. Monogr. 44:153–169, 1974), especially small ones. While the Slender Antbird has dense populations and may resist extinction, it could be lost.

Acknowledgments.—We appreciate a grant from the Committee for Research and Exploration of the National Geographic Society, the courtesy of ranchers Joel Almeida Sampaio and Humberto Gomes Sampaio of Fazenda Alvorada and of other people of Boa Nova and information furnished by the agronomists of CEPLAC at Itabuna. Eugene Eisenmann and John Farrand checked the records of *Rhopornis* and suggested the correct Boa Nova for us. Edwin O. Willis and Yoshika Oniki, *Dept. Biology, Univ. Miami, Coral Gables, Florida 33124.* *Accepted 15 Jan. 1980.*

Wilson Bull., 93(1), 1981, pp. 107–108

Notes on the Uniform Crake in Costa Rica.—Although the Uniform Crake (*Amaurolimnas concolor*) is found from Mexico to Bolivia and Brazil, and formerly occurred on Jamaica, virtually nothing is known of its habits. During fieldwork in 1971–1973 at Finca La Selva, in the wet lowlands of NE Costa Rica, I obtained information on the behavior and vocalization of this elusive bird, as well as the first unequivocal data on nesting of the species.

Although not reported for La Selva by Slud (Bull. Am. Mus. Nat. Hist. 121:49, 1960), the Uniform Crake is fairly common in forested swamps, heavy vine-tangled thickets along forested streams and in dense second growth adjoining forest, especially favoring the maze of hanging dead and decaying leaves in *Heliconia* thickets (cf. also Orians and Paulson, Condor 71:426, 1969; Kiff, Condor 77:101, 1975). In these dense, tangled habitats, the birds are not particularly shy and may approach a motionless observer closely, but seldom leave the densest available cover.

In life, *A. concolor* resembles a diminutive wood-rail (*Aramides* sp.) in build, posture and soft-part colors: red iris, greenish-yellow bill and orange to reddish legs. The bird usually has an erect stance and walks with head high and tail cocked, except while foraging. The tail may be pumped in agitation and is carried low as the bird scurries, mouselike, across an opening. The birds forage deliberately, walking slowly and pecking into leaf litter, hanging dead leaves and detritus. Apparently they also dig in soft mud, as I have observed birds with obviously muddy beaks on several occasions. I have seen Uniform Crakes seize, beat and swallow spiders (Lycosidae), a very small frog (*Eleutherodactylus* sp.) and a small lizard (*Anolis* sp.), which was killed with a few swift pecks, then swallowed headfirst.

Like *Aramides* wood-rails, the Uniform Crake possesses loud, arresting whistled calls that often provide the only clue to its presence. To date I have noted the following vocalizations:

(a) A series of 6–9 clear, upslurred whistles, in which successive notes first become louder and higher pitched, then accelerate, drop in pitch and fade away—*tooeee*, *Tooeee*, *Toooeee*, *TOOOEEE*, *Tooee*, *tooee-tuee-tui*. A bird giving this call was often answered by another some distance away. I could often decoy single birds to within 1–2 m by imitating it; this call is probably a territorial advertisement or "song." At very high intensities (as when answering my imitation at very close range), the loudest notes of the call often had a flutelike break in the middle: *toourleee*, etc.

(b) At close range in the last-mentioned situations a soft, low-pitched, pigeon-like *cuuuuhuuuu* is audible, possibly an aggressive note.

(c) Two birds, perhaps a mated pair, may call back and forth with one or several clear, not very loud, whistled *toooo* notes, either level in pitch or slightly downslurred.

(d) A sharp, nasal *kek* is given by a startled bird.

The loud "song" of *A. concolor* was heard at La Selva chiefly from late August to December, which is probably the breeding season. On 14 November 1973, I found a nest with eggs in an area where I had seen and heard much *A. concolor* activity in the preceding 2 months.

The nest consisted of a loose cup of leaves filling a hollow in the top of a vine-covered stump beside a seldom used trail in a small treefall clearing in swamp forest. The stump was about 5 m from a stream, and 1 m from the nearset dense thicket, into which the adult bird flushed from the nest promptly disappeared, allowing a brief glimpse of reddish-brown plumage and orange legs. The nest contained 4 slightly incubated, sub-elliptical, slightly glossy eggs (set no. 78177 of the Western Foundation of Vertebrate Zoology). The ground color of the eggs is pale buffy, marked mostly near the large end with bold superficial reddish-brown splotches and subsurface spots and blotches of grey and purplish-brown. Measurements (length and largest diameter) and dry shell weights of each egg are: 33.40 × 26.11 mm, 0.774 g; 44.41 × 25.90 mm, 0.740 g; 33.28 × 26.18 mm, 0.789 g; and 33.60 × 25.74 mm, 0.675 g.

The first description of a putative *A. concolor* egg (from Brazil) was by Nehrkorn (Katalog der Eiersammlung nebst Beschreibungen der Aussereuropäischen Eier von Adolf Nehrkorn, 11 Auflage, R. Friedländer und Sohn, Berlin, 1910): "reddish-grey with very sparse violet and rust-brown flecks, 33 × 26.5 mm" (translation mine). The measurements, but not the colors, fit the set described here. Schonwetter (Handbuch der Oologie, Lieferung 5, Akademie-verlag, Berlin, 1961) repeated Nehrkorn's description but could not locate the egg in question, which is probably lost. Bond (Birds of the West Indies, Waverly Press, Baltimore, Maryland, 1936) wrote of *A. concolor* that "the egg of the continental form is said to be ashy-grey with a reddish tinge, speckled dusky (34 × 31.5 mm)." This description was not repeated in later editions of Bond's book, and its original source is unknown; since neither colors nor measurements agree with the present set, the identification was probably erroneous. Finally, Wetmore (Birds of the Republic of Panama, Pt. 1, Smithson. Misc. Coll. Vol. 150, 1965) described eggs he believed to pertain to *A. concolor* collected on Isla San José, in the Las Perlas Archipelago off the Pacific coast of Panama on 1 September 1944. The description, measurements and date agree well with the present set, but as the eggs had been picked up by a worker who stated only that they "had been found in a low nest," the identification clearly required corroboration.

The eggs of *A. concolor* are quite similar to those of *Rallus* spp. and *Aramides* spp., but differ markedly in these respects from eggs of *Laterallus* spp. or *Porzana* spp. Behavior and vocalizations of *Amaurolimnas* also indicate close affinities with *Aramides*, as suggested by Olson (Wilson Bull. 85:381, 1973). Peters (Birds of the World, Vol. 2, Harvard Univ. Press, Cambridge, Massachusetts, 1934) had placed *Amaurolimnas* among a group of probably unrelated Old World genera. Ripley (Rails of the World, David Godine, Boston, Massachusetts, 1977) recognized an *Amaurolimnas-Aramides* relationship by lumping both into the Old World *Eulabeornis*. Relationships to Old World rails are beyond the scope of the present paper, but my observations definitely support the conclusion that *Aramides* is the closest relative of *Amaurolimnas*.

I thank L. F. Kiff for supplying weights and measurements of the eggs of *A. concolor* and for bibliographic assistance and critical commentary. K. C. Parkes and S. Olson suggested several improvements in the manuscript and S. M. Smith provided help in the field. Work at La Selva was supported financially by a Chapman-Naumberg Postdoctoral Fellowship from the American Museum of Natural History, and logistically by the Organization for Tropical Studies.—F. G. Stiles, *Escuela de Biología, Universidad de Costa Rica, Cuidad Universitaria, Costa Rica, Central America.* *Accepted 14 Jan. 1980.*

Wilson Bull., 93(1), 1981, p. 109

Trichomoniasis in Bald Eagles.—The protozoan parasite *Trichomonas gallinae* has been reported causing disease in the upper digestive tract of a variety of birds including the Golden Eagle (*Aquila chrysaetos*); the Rock Dove (*Columba livia*) is its primary host (Levine, Protozoan Parasites, Burgess Publishing Co., Minneapolis, Minnesota, 1973). This flagellate, in birds of prey, causes a disease called "frounce," characterized by yellow caseous nodules in the upper alimentary canal and emaciation (Stabler, Exper. Parasitol. 3:368–402, 1954). This note reports 2 cases of trichomoniasis found in Bald Eagles (*Haliaeetus leucocephalus*) that were subsequently treated with Emtryl (1,2-dimethyl-5-nitroimidazole, Dr. Salsbury's Laboratory, Charles City, Iowa). Stabler and Kitzmiller (N. Am. Falcon. J. 7:47–48, 1967) recommend this drug as a safe and effective treatment for trichomoniasis in hawks.

On 25 February 1977, a debilitated 6.3 kg adult Bald Eagle was found in Sullivan County, New York. The bird was treated for shock and given an antibiotic by a veterinarian. When the senior author examined the bird on 27 February 1977, yellow-brown caseous lesions were present over most of the surface of the hard palate, and the saliva was blood-tinged. Numerous live trichomonads were demonstrated microscopically from the lesions and saliva, and lesion smears stained with Giemsa stain showed organisms fitting the description of *T. gallinae* (Levine 1973). The bird was given orally three 125 mg tablets of Emtryl. On 1 March 1977, the mouth lesions were nearly gone. However, rare trichomonads were found microscopically from material taken from the esophagus on 4 March and 3 more 125 mg tablets were given. This was repeated on 5 March. No ill effects were noted from the medication. The eagle rapidly gained strength and showed greatly increased aggression toward its caretakers. Further examination for trichomonads were negative, and the bird was released to the wild on 11 March.

The second Bald Eagle was an immature, captured in a weak, emaciated condition in a farm field near Cutchogue, Suffolk Co., Long Island on 26 July 1978, after it flew weakly against a slow moving pick-up truck. This bird was treated for shock and x-rayed at the North Fork Animal Hospital, Southhold, Long Island. No broken bones, or reason for the sickness were found. On 28 July 1978, the bird was transferred to the Delmar Wildlife Resources Center at Delmar, New York. The eagle was thin (3.6 kg), weak and had numerous yellow-brown circumscribed lesions on the hard palate, pharynx, tongue and anterior esophagus. Microscopic examination of oral scrapings revealed numerous organisms typical of *T. gallinae*. Five hundred mg of Emtryl were administered to the bird on 28 July by mouth. The dose was repeated 24 h later as the lesions were disappearing. The eagle showed no untoward effects from an approximate dose of 278 mg of Emtryl per kg of body weight given in a 24 h period. The bird fed voraciously on venison and fish, and appeared stronger. On 31 July the lesions had almost entirely healed and the bird was given another 250 mg of Emtryl. No trichomonads could be found in the mouth or esophagus. The bird gained weight and vigor, remained negative for trichomonads and was released on 10 August at Shelter Island, New York.

The eagles may have contracted the trichomoniasis from eating Rock Doves and/or Mourning Doves (*Zenaida macroura*). Tangredi (N.Y. Fish and Game J. 25:89–90, 1978) reported trichomoniasis in Mourning Doves from Long Island, and many Rock Doves were seen near the capture site of the eagle from Sullivan County.

These seem to be the first cases of trichomoniasis reported in the Bald Eagle. Emtryl appears to be a very quick and effective way to eliminate trichomoniasis in this species.—Ward B. Stone and Peter E. Nye, *N.Y.S. Dept. Environmental Conservation, Delmar Wildlife Resources Center, Delmar, New York 12054.* *Accepted 27 Nov. 1979.*

Wilson Bull., 93(1), 1981, p. 110

***Protocalliphora* infestation in Broad-winged Hawks.**—In spring and summer 1978, during study of the productivity of the Broad-winged Hawk (*Buteo platypterus*) in Chautauqua County, New York, we discovered infestation of nestlings by dipteran larvae later identified as *Protocalliphora avium* Shannon and Dobroscky (Calliphoridae). This is the first reported occurrence of infestation of the Broad-winged Hawk by this ectoparasite. Bohm (Wilson Bull. 90:297, 1978) listed *Protocalliphora* spp. in Great Horned Owls (*Bubo virginianus*), Long-eared Owls (*Asio otus*), Red-tailed Hawks (*Buteo jamaicensus*), Red-shouldered Hawks (*Buteo lineatus*) and Cooper's Hawks (*Accipter cooperii*).

Larvae were first noticed and collected from the ear cavities of nestling broad-wings from 18–26 days old. Each nestling in 3 broods of 2 averaged 9 larvae (range 2–15) per pair of ear cavities. Three nestlings in an additional brood, killed by a predator at 6–9 days of age, were not infested. The infested nests were widely separated, and the nest-sites were variable in characteristics.

The nestlings appeared to suffer no major deleterious effects from infestation by the blood-sucking larvae. However, bleeding was observed in the ear cavities, the skin around the ear openings was swollen and scabs sometimes covered the ear cavities. No behavioral abnormalities were noticed. Bohm (1978) stated that infestation by these dipterans caused no serious harm to large species, but did cause some mortality in small passerines. Because mortality is known in small birds, and because at least 1 other ectoparasite (Mexican chicken bug [*Haematosiphon indorus*]) is known to cause nestling mortality in raptors (Platt, Wilson Bull. 87:557, 1975), *Protocalliphora* might be expected to cause or contribute to mortality of small or undernourished nestling Broad-winged Hawks, and potentially other raptor nestlings. The effects of ectoparasites should be looked for in bird species showing brood reduction strategies for growth and reproduction (see O'Conner, Living Bird 16:209–239, 1977) in which the young are often undernourished and weak, and this includes raptors.

We wish to thank Allen Benton, Robert Bohm and especially C. W. Sabrosky for their aid in identifying the larvae.—Scott Crocoll and James W. Parker, *Dept. Biology and Environmental Resources Center, State Univ. Coll., Fredonia, New York 14063.* *Accepted 30 Oct. 1979.*

Wilson Bull., 93(1), 1981, pp. 110–111

Herring Gull attacks and eats adult male Oldsquaw.—Herring Gulls (*Larus argentatus*) have been observed preying on a wide variety of small adult birds (Witherby, Jourdain, Ticehurst and Tucker, The Handbook of British Birds, Vol. 5, H. F. and G. Witherby Ltd., London, England, 1952; Harris, Ibis 107:43–53, 1965). Such prey items are almost always small passerines or shorebirds, and as such are much smaller than the gulls themselves. Harris (1965) mentions Herring Gull predation on Manx Shearwaters (*Puffinus puffinus*), Razorbills (*Alca torda*) and Common Puffins (*Fratercula arctica*), and Peter Fetterolf (pers. comm.) has observed Herring Gulls preying on juvenile Ring-billed Gulls (*L. delawarensis*). Few, if any, instances of Herring Gulls preying on birds larger than these have been reported. This note reports an instance of predation on an adult male Oldsquaw (*Clangula hyemalis*) by an adult Herring Gull. The average weight of an adult male Oldsquaw in December is about 580 g (Peterson and Ellarson, Wilson Bull. 91:288–300, 1979). The average weight of an adult Herring Gull is 1098 ± 151 g, based on a sample of 15 male and 11 female specimens at the Royal Ontario Museum, Toronto, Canada.

Daily mid-December populations of Oldsquaws in the inner harbor at Toronto, Ontario, average about 1500 individuals (Alison, M.Sc. thesis, Univ. Toronto, Toronto, Ontario, 1970). On 28 December 1978, at 10:23, while watching Oldsquaw behavior at about 1000 m from the 30 m Toronto Harbor Police observation tower with a 20× spotting scope, I observed an adult Herring Gull attack an adult male Oldsquaw. The gull dived at and struck the duck from a height of 20–30 m. Similar attacks were observed at 11:00, 11:19 and 11:55 and others may have occurred. The Oldsquaw was never observed diving or flying and swam only when attacked. At 12:06, all the Oldsquaws (>100 individuals) within 1500 m flocked and flew in a tight 50–100 m diameter circle above the stricken duck. The Herring Gull, having apparently killed the duck, was seen using its bill to bite and pick at the carcass, apparently feeding; after about 3 min the flock of circling Oldsquaws began to disperse. The gull alternately swam within 3 m of the Oldsquaw carcass or fed on it until 12:47, at which time the gull departed. At 13:01, either it or another Herring Gull landed beside the carcass and remained within 3 m of it occasionally feeding until 14:17, when the gull departed. No subsequent visits to the carcass were made by Herring Gulls or any other birds, and by 14:40 the duck was no longer visible. Presumably it sank; Schorger (Wilson Bull. 59:151–159, 1947) reported that Oldsquaws with completely water saturated plumage have negative buoyancy.

I thank the Toronto Harbor Police for permitting access to their tower. Comments and criticism by P. M. Fetterolf, J. D. Rising, N. J. Flood, G. R. Bortolotti and J. C. Barlow are appreciated.—Richard R. Snell, *Dept. Zoology, Univ. Toronto, Toronto, Ontario M5S 1A1 Canada.* *Accepted 30 Jan. 1980.*

Wilson Bull., 93(1), 1981, pp. 111–112

Red-legged Kittiwakes forage in mixed-species flocks in southeastern Alaska.— The foraging behavior of Red-legged Kittiwakes (*Rissa brevirostris*) away from their breeding sites is virtually unknown. Between 1–7 September 1978, we observed adult and juvenile Red-legged Kittiwakes foraging in a mixed-species flock of adult Mew Gulls (*Larus canus*), juvenile Bonaparte's Gulls (*L. philadelphia*) and juvenile Glaucous-winged Gulls (*L. glaucescens*) in the lower Green's Creek drainage on Admiralty Island in southeastern Alaska.

During ebb tide the exposed delta mud flats at Green's Creek are used by thousands of gulls and shorebirds, particularly during spring and fall migration. The lower portion of Green's Creek is used by spawning salmon during late July through September: hundreds of humpbacked salmon (*Oncorhynchus gorbusche*) were present during our observations.

We observed 5 mixed-species flocks of about 50 individuals each at the open meadow bordering Green's Creek, always during ebb tide; never when the stream bank and adjacent meadow were flooded. The flock composition was nearly constant: Glaucous-winged Gulls, 10%; Mew Gulls, 25%; Bonaparte's Gulls, 35%; and Red-legged Kittiwakes, 30% (adults, 10%; juveniles, 20%). (The identification of the kittiwakes in the flocks was difficult at first; however, the juveniles were discriminated from juvenile Bonaparte's Gulls by the kittiwakes' well-marked, dark cervical collar, their dusky eyes, and unbarred tail. The adult kittiwakes differ from adult Mew Gulls by their solid black wing tips and red legs.) Glaucous-winged Gulls arrived first and remained near the deep, still water or the gravel shore, coming closest to the forest edge. Mew Gulls arrived next, followed soon by Bonaparte's Gulls. Red-legged Kittiwakes were the last to arrive, and they frequented the faster stream riffles and stayed farthest from the forest edge. Mew and Bonaparte's gulls always stayed between the Glaucous-winged Gulls and Red-legged Kittiwakes. None of the gulls or kittiwakes left the stream banks, nor flew into the forest. We observed no interactions between species.

Glaucous-winged and Mew gulls spent most of their time sitting on the water or the rocky shore. They pecked the exposed dorsal surface of the spawning salmon, but we could not confirm feeding. Bonaparte's Gulls and Red-legged Kittiwakes flew almost continuously and dived frequently. Bonaparte's Gulls appeared to be "pursuit diving," and the kittiwakes, "dipping" (terms from Ashmole, pp. 223–286 *in* Avian Biology, D. A. Farner and J. R. King, eds., Academic Press, New York, New York, 1971). Close observation showed that kittiwakes generally dived between salmon and ate something from the stream bottom, presumably salmon eggs. On at least 2 occasions, kittiwakes pecked at the exposed dorsal surface of salmon spawning in the stream. Although dead salmon were abundant on sand banks, we never saw gulls or kittiwakes eat any of them.

Adult and juvenile kittiwakes foraged similarly. No pattern of dominance, aggression, or indication of feeding hierarchy was detected. Juveniles foraged next to, and independent of, adults.

Red-legged Kittiwakes are commonly found near the Pribilof Islands during the breeding season; they are rare, post-breeding visitors to the northeastern Bering Sea and Aleutian Islands. There are a few accidental records in southeastern Alaska and the Yukon River (Kessel and Gibson, Stud. Av. Biol. 1:48–49, 1978), but they are usually seen at sea, if at all. They have only been reported to feed on small fish and cephalopoda in the waters south of the Pribilofs (Hunt, pp. 196–382 *in* Environmental assessment of the Alaskan continental shelf, Vol. 2, Natl. Ocean. Atmos. Admin. Environ. Res. Lab., Boulder, Colorado, 1977).

Bonaparte's and Mew gulls are common visitors to southeastern Alaska in fall, and the Glaucous-winged Gull breeds there—it probably is not unusual to find these 3 gulls foraging together (Bent, U.S. Natl. Mus. Bull. 113:65–73, 1921). Our observations are significant in that range extensions in both location and time are established for the Red-legged Kittiwake, and the post-breeding feeding habits in southeastern Alaska are described for the first time.

This study was partially supported by VTN, Inc. We thank V. Byrd, G. Hunt, K. Vermeer and the Editor for helpful comments.—Douglas Siegel-Causey, *Dept. Ecology and Evolutionary Biology, Univ. Arizona, Tucson, Arizona 85721* and Thomas E. Meehan, *VTN Consolidated, Inc., 2301 Campus Dr., Irvine, California 92713.* *Accepted 10 Feb. 1980.*

Wilson Bull., 93(1), 1981, pp. 112–114

Ground-feeding methods and niche separation in thrushes.—Recent papers by Clark (Wilson Bull. 83:66–73, 1971) and Henty (Wilson Bull. 88:497–499, 1976) have described a foraging method used by a number of species of birds, consisting of lateral sweeps of the bill to move aside loose material. They termed it "bill-sweeping" and reported its occurrence in several thrushes (*Turdus*), namely the White-necked Thrush (*Turdus albicollis*), European Blackbird (*T. merula*), American Robin (*T. migratorius*) and Songthrush (*T. philomelos*). I have recently observed such behavior, together with other foraging methods, in 2 additional species, the Fieldfare (*T. pilaris*) and European Redwing (*T. iliacus*) and incidentally in the European Blackbird. The intention of this note is to relate bill-sweeping to other principal foraging techniques used by thrushes when feeding on the ground, and to comment on niche separation in the genus.

Observations were made between October 1975 and February 1976 on wild birds in Cambridgeshire, England, using a hide or vehicle stationed at the edge of a field. Birds regularly approached to within 20 m, and sometimes to within 10 m of a concealed observer, providing detailed views of their searching and handling techniques.

Table 1
Relative Use of Food Categories by Fieldfares and Redwings

	Fieldfare N (%)	Redwing N (%)
Surface items (all <10 mm long)	266 (43.7)	176 (66.9)
Soil items	342 (56.3)	87 (33.1)
Soil items >10 mm long	154 (45.0)	19 (21.8)

The 2 main species were wintering together on areas of cattle-grazed permanent pasture. For most of the winter this was their preferred habitat, in which they collected invertebrate food. Foods taken comprised 2 major categories: (1) "soil items," including earthworms, centipedes, slugs and larvae of beetles and craneflies (Tipulidae), which required extraction from soil or grass tufts; and (2) "surface items," exposed on the soil or vegetation, and comprising mainly flies, beetles and spiders, for which handling was minimal. This division was based on the difference in technique required for the capture of prey items in each category.

Similar methods were used by both Fieldfares and Redwings when taking prey from a given category. In both species searching for both categories consisted of running along the ground in short bursts, usually of 1–5 paces or hops, halting after each run, and apparently scanning the ground in the immediate vicinity. If a potential food item was spotted, a few paces might be taken towards it. In the case of a surface item the bird usually pecked immediately at it (although there might be a brief hesitation) during which the bird might cock its head to one side before the peck. Occasionally, more than 1 peck was made. With a soil item, the behavior was similar to the bill-sweeping described by Clark (1971), although he found bill-sweeping used "to move aside twigs, leaves, dry soil, or snow" and did not mention use on relatively hard-packed substrates such as the damp soil with dense roots found on the present study area. On hard substrates the behavior is more appropriately termed digging, as described by Heppner (Condor 67:247–256, 1967) for American Robins hunting earthworms. As in robins, a Redwing or Fieldfare would stop near potential prey, hesitate, often cocking the head to one side, sometimes take a short step backwards or to one side, then stab downwards. Often several pecks were made, when the first few did not usually secure the food. Instead the downward stab was followed by a head flick, often causing soil to be thrown to one side. The flick might be more or less pronounced, and occasionally was not lateral.

The major difference between the bill-sweeping described by Clark (1971) and Henty (1976) and digging as described by Heppner (1967) and the present paper is that the former is a search technique while the latter is a "pursuit" technique used after a potential prey has been spotted. However, the two are seemingly related.

Bill-sweeping was also used by Fieldfares and Redwings to move aside loose material. Redwings occasionally fed in dead leaves in the manner described by Henty (1976), walking through the litter with almost continuous, rapid, lateral head movements. Redwings used a similar method when searching cattle dung for dipteran larvae, except the bird stood still by a pat while searching. When Redwings foraged in cowpats in this way, the technique was intermediate in action between bill-sweeping and digging, and was used for both search and "pursuit." Fieldfares searched litter much less frequently than Redwings, and were never observed feeding at cowpats.

The 2 species differ in size—the Fieldfare weighing 120–140 g and the Redwing 60–80 g. These differences were reflected in differences in diet. I recorded the numbers of surface and soil items taken by thrushes in many large flocks over the whole winter (Table 1). In order to avoid bias due to observations containing different numbers of items captured I calculated the proportion of surface items taken during each feeding record. A Mann-Whitney *U*-test on the difference of this proportion between the species was highly significant ($P < 0.001$). The Redwings took more surface items than soil items and the Fieldfares took more soil items than surface.

Digging required more time and energy than picking items from the grass. However, soil items were generally larger than surface items (Table 1); also Fieldfares took larger soil items than did Redwings (Table 1, Mann-Whitney *U*-test, $P < 0.01$).

Thus, the 2 species subdivided the habitat primarily on spatial and behavioral differences; differences in prey size were to some extent consequential upon these, supporting Hespenheide (pp. 158–180 *in* Ecology and Evolution of Communities, M. L. Cody and J. M. Diamond, eds., Belknap Press, Harvard, Cambridge, Massachusetts, 1975). However, prey size differences were also evident within a foraging zone, indicating either that each species had prey-size preferences or that some undetected difference in foraging technique was involved (such as depth of digging).

In late February and March, when the availability of larger insects on the surface and vegetation increased (Tye, unpubl.), the Fieldfare took proportionately more surface items (75.4%) than in winter (43.7%, October to mid-February) and more closely resembled the Redwing in feeding techniques, suggesting that prey-size preferences may have been important in determining the Fieldfare's feeding behavior.

Litter-feeding was most common when the ground was frozen or snow-covered. At such times most Fieldfares left the study area completely, and the remaining few fed on small clear patches of pasture or garden lawns. In contrast, Redwings moved into hedge-bottoms and gardens and switched to litter-feeding. Prey items found in litter resembled surface items of the open pasture, mostly small arthropods and slugs. Large items were uncommon in the litter which may explain why Fieldfares did not often feed there.

The European Blackbird apparently used the same techniques as the Fieldfare and Redwing, if not in the same proportions. The Blackbird tended to bill-sweep in a strict sense more than the Fieldfare, especially in litter, and to dig more than the Redwing, and was probably intermediate in its use of soil and surface items on pastures. It is also intermediate in size (ca 90–120 g).

Therefore, when feeding on the ground, the *Turdus* species studied so far all seem to use the same range of related feeding techniques. Within a habitat they achieve niche separation by the differential use of these techniques, and therefore of the foraging zones for which each technique is appropriate. Further niche separation may also be achieved by prey-size preferences within a foraging zone. The behavioral, spatial and prey size differences may be related to body size.

These observations were made while working for a Ph.D., supervised by the late Prof. R. K. Murton and Dr. P. P. G. Bateson, at Monks Wood Experimental Station, and financed by a Natural Environment Research Council Studentship. P. P. G. Bateson, J. C. Barlow, J. P. Dempster, I. Newton and N. J. Westwood commented on the manuscript. N. J. Westwood provided some bird weights.—Alan Tye, *Monks Wood Experimental Station, Abbots Ripton, Huntingdon PE17 2LS, Cambridgeshire, England.* (Present address: *Dept. Zoology, Fourah Bay Coll., Univ. Sierra Leone, Freetorun, Sierra Leone.*) *Accepted 20 Feb. 1980.*

Wilson Bull., 93(1), 1981, pp. 115–118

American Coot distribution and migration in Colorado.—American Coots (*Fulica americana americana*) are widespread in North America, breeding primarily on fresh water wetlands and wintering on both brackish and fresh water habitats (Fredrickson, *in* Management of Migratory Shore and Upland Game Birds in North America, Sanderson, ed., Int. Assoc. Fish and Wildl. Agencies, Washington, D.C., 1977).

Despite being one of the more common marsh birds and a game species, the coot is often overlooked or ignored during waterfowl inventories or marsh evaluations. Current data concerning the coot in Colorado are limited. Cooke (The Birds of Colorado, Colo. Agric. Exper. Stat. Bull. 37, 1897), Keyser (Birds of the Rockies, McClory & Co., Chicago, Illinois, 1902), Sclater (A History of the Birds of Colorado, Witherby and Co., London, England, 1912), Niedrach and Rockwell (The Birds of Denver and Mountain Parks, Colo. Mus. Nat. Hist. Pop. Ser. No. 5, 1939) and Bailey and Niedrach (Birds of Colorado, Denver Mus. Nat. Hist. Vol. I, 1965) summarized general information on nest observations, early and late occurrences and distribution. More recently Kingery and Graul (Colorado Bird Distribution Latilong Study, Colo. Field Ornithol. and Colo. Div. Wildl., Denver, Colorado, 1978) updated distribution data and Lane and Holt (A Birder's Guide to Eastern Colorado, L & P Press, Denver, Colorado, 1979) gave average arrival and departure dates for eastern Colorado. We initiated surveys of wetlands in August 1976 to further delimit distribution, seasonal abundance and aspects of coot biology in Colorado.

Study areas and methods.—Counts of coots were conducted on 4 study areas to document spring and fall migration. Study areas were selected to represent the major topographic areas of Colorado and were located at Beebe Draw near LaSalle, Weld Co., on the eastern plains; Lake John, near Walden, Jackson Co., in North Park; Ice Pond, near Buena Vista, Chaffee Co., in the central mountains; and Hog Lake, part of Brown's Park National Wildlife Refuge (NWR), Moffat Co., in extreme northwestern Colorado. Each study area included an emergent marsh dominated by cattail (*Typha* spp.) and/or bulrush (*Scirpus acutus*) and areas of open water.

Weekly counts were initiated in 1977 to document spring migration at Beebe Draw and Lake John. Ice Pond and Hog Lake were not visited until after the peak of migration. However, counts by Brown's Park National Wildlife Refuge personnel from 14 March to 22 May 1977 were used to indicate coot migration at Hog Lake. In 1978, regular visits to all areas began by mid-March.

Distribution and status were determined from 108 questionnaires returned by field personnel of the Colorado Division of Wildlife and amateur ornithologists and by observations of 230 wetlands encountered while traveling between study areas throughout the state from August 1976 through November 1978. Most regions of the state were visited, with the exception of the far eastern plains, especially along the South Platte and Arkansas rivers.

Date or period of observation, dominant emergent vegetation, geographic location, coot numbers and status (breeding, resident, migrant only, etc.) were recorded for each wetland visited. Vegetation was classified as either cattail and/or bulrush, or other. Omitted were roadside ditches and wetlands completely filled with cattail and/or bulrush with no open water. "Other" included areas with sedges (*Carex* spp.), willows (*Salix* spp.), or grasses (Graminae) as the dominant emergents, or areas without any emergents, such as many lakes, reservoirs, and stockponds. Geographic location classifications were eastern plains, high mountain valleys and west of the Continental Divide. High mountain valleys refer specifically to North, Middle and South parks (large inter-mountain depressions devoid of extensive woodlands) and the San Luis Valley. Coots were considered to be breeding if territorial

Table 1

Relationship of Coot Breeding Distribution and Vegetation Type in Colorado

Area	Number of areas surveyed						χ^2 (df = 1)	Probability
	Dominated by *Typha* or *Scirpus*			Dominated by other vegetation				
	With breeding coots	None or nonbreeders	Total	With breeding coots	None or nonbreeders	Total		
Statewide	45	31	76	15	136	151	63.13	<0.001
Eastern plains	17	10	27	1	58	59	42.02	<0.001
High mountain valleys	8	1	9	13	35	48	12.44	<0.001
West of Continental Divide	20	20	40	1	43	44	25.45	<0.001

behavior (as defined by Gullion, Wilson Bull. 64:83–97, 1952) and nests and/or young coots were observed during 15 April through 15 August, and nonbreeding if gregarious and nonterritorial. Coots observed from 16 August through 14 April were classed as migrating or wintering. Distribution and status classifications were assigned according to the latilong system (Kingery and Graul 1978), with the state divided into 27 blocks based on lines of latitude and longitude.

Distribution and status.—Coots bred throughout most of Colorado. Breeding was not documented in 2 latilong blocks, one located in the southcentral mountain region and the other in the southeastern plains. Major breeding areas were Brown's Park on the western slope, and North Park and the San Luis Valley in the high mountain valleys. Breeding coots were not observed in Middle or South parks, although previously reported (Cooke 1897, Lane and Holt 1979) and to 3045 m elev. at Kenosha Pass (Bailey and Niedrach 1965). On the plains, coots were locally abundant where suitable habitat occurred.

Nesting coots were primarily associated with cattail and bulrush marshes (Table 1). A Chi-square test of independence between the presence or absence of breeding coots and the occurrence of cattail and/or bulrush dominated marshes indicated a strong relationship ($P < 0.001$) in each region and statewide. A similar analysis for the migration-wintering period also indicated a strong relationship ($P < 0.001$) statewide. Not all cattail or bulrush marshes were used by breeding, migrating or wintering coots, but they were used in strong preference to other vegetation types. Other vegetation types used for nesting included tamarix (*Tamarix gallica*), spikerush (*Eleocharis macrostachya*), willows and sedges. Sedges growing as emergents were characteristic of many high elevation wetlands used by coots, especially wetlands in North Park.

Coots were resident in low numbers (< 1000), mainly along the western boundary of the plains from near Fort Collins south to Pueblo. The presence of wintering coots was dependent on mild winter weather. Coots were present near Fort Collins during the winter of 1976–77, but absent during the 1977–78 winter when water areas froze. In the Fort Collins area, coots associated with wintering waterfowl and fed on feces and waterfowl carcasses. Christmas bird counts sponsored by The National Audubon Society (1960–1977) and listed in Audubon Field Notes and American Birds have consistently noted coots along the Front Range from Fort Collins to Pueblo.

Spring migration.—At Beebe Draw and Hog Lake coots arrived in late February or early

Table 2

Total Number of Coots Observed During Spring and Fall Migrations 1977 and 1978, 4 Study Areas, Colorado

Location	Month and week											
	March				April				May			
	1	2	3	4	1	2	3	4	1	2	3	4
Beebe Draw 1977	—	15	58	105	132	178	168	115	81	54	50	95
Beebe Draw 1978	0	5	17	32	58	98	94	88	80	48	56	58
Lake John 1977	—	—	—	—	0	146	851	706	394	172	172	199
Lake John 1978	—	0	0	0	0	304	688	689	—	305	—	124
Ice Pond 1977	—	—	—	—	—	—	—	305	—	—	75	85
Ice Pond 1978	—	31	79	184	222	264	348	271	—	280	—	59
Hog Lake 1977	—	100	—	500	—	680	—	—	345	—	280	200
Hog Lake 1978	35	179	307	489	674	846	782	646	—	351	—	105

Location	Month and week											
	August				September				October			
	1	2	3	4	1	2	3	4	1	2	3	4
Beebe Draw 1977	39	46	63	72	—	141	127	114	—	—	19	0
Beebe Draw 1978	—	90	130	179	—	267	393	532	—	520	603	214
Lake John 1977	911	987	990	1279	2477	2680	3255	1964	2648	2290	1995	1779
Lake John 1978	—	367	525	695	865	1252	2340	2836	2694	2255	3141	1766
Ice Pond 1977	151	—	269	326	346	443	406	395	306	192	—	96
Ice Pond 1978	—	123	170	184	218	222	274	251	222	207	136	107
Hog Lake 1977	—	—	575	273	518	367	402	435	336	301	—	215
Hog Lake 1978	—	345	307	368	577	499	652	620	678	549	422	349

March. Peak numbers were recorded in 1977 and 1978 during the second week of April (Table 2). At Lake John coots arrived in 1977 and 1978 during the second week of April, although coots were present elsewhere in North Park the previous week. Arrival date was dependent on ice thaw. In both years numbers increased rapidly for 2 weeks, then decreased to resident levels within 3–4 weeks. Although coots arrived at Ice Pond earlier than Lake John, peak numbers were also recorded the third week of April. The decrease of coot numbers from peak to resident levels in 1977 and 1978 was consistent with other areas.

Timing of migration and relative numbers observed on each area were consistent between years. The general pattern statewide was arrival in late February or early March (first week of April at Lake John), increasing to peak numbers during the second to third week of April, then decreasing to resident levels by the second to fourth week of May. Timing of peak migration was similar for the eastern plains and west of the Continental Divide. The peak occurred 1 week later in the high mountain valleys. The literature suggests a similar pattern of coot migration in Colorado.

Summer movements.—Numbers of adult coots increased gradually on the study areas and/or peripheral marshes starting in mid- to late July. Increases in numbers of immature coots 30 days of age or older occurred in mid- to late August. An influx of adult and immature coots on Hog Lake in 1977 began about 2 weeks earlier than the general pattern found on other areas.

The late summer buildup was influenced by local conditions. Adult and immature coots will leave a marsh as water levels recede and it dries (Ryder, Ph.D. thesis, Utah State Univ., Logan, Utah, 1958). This situation was particularly applicable to Beebe Draw and Hog Lake, where breeding coots occurred on nearby marshes. Movements onto Hog Lake were in part related to pumping schedules and water levels on nearby marshes. Water levels were allowed to recede on some marshes in Brown's Park NWR as the summer progressed. Immature coots crossed the Green River in the direction of Hog Lake on at least 1 occasion.

Fall migration.—Peak numbers were recorded in 1977 on all areas during late August to mid-September, before the waterfowl hunting season of 1–14 October (Table 2). In 1978, peak numbers were observed 5 weeks later at Beebe Draw, 2 weeks later at Lake John, 1 week later at Ice Pond and 6 weeks later at Hog Lake. Peak numbers occurred before the 30 September–13 October 1978 waterfowl season at Ice Pond and during or after the hunting season for the other areas. In November 1977 and 1978, coot numbers decreased to minimal levels. No coots were known to winter on the study areas.

Compared to spring, fall migration occurred over a more widespread period, with less dramatic changes in numbers and with less consistency in timing. Successive migratory waves may explain the fluctuating numbers observed on some Colorado areas.

Acknowledgments.—Financial assistance was provided by the Accelerated Research Program for Migratory Shore and Upland Game Birds and the Colorado Division of Wildlife, Federal Aid to Wildlife Restoration Project W-88-R. We are grateful to J. Creasey, refuge manager, Brown's Park National Wildlife Refuge, and his staff, G. Deutscher and J. Sellers, for their assistance throughout the field investigations. We thank the Beebe Draw Gun Club for access to its property and the Mt. Princeton Fishing Club, especially R. M. Stabler for access to Ice Pond. Gratitude is expressed to all who returned questionnaires concerning coot observations in Colorado.—WARNER P. GORENZEL, RONALD A. RYDER, *Dept. Fishery and Wildlife Biology, Colorado State Univ., Fort Collins, Colorado 80523* AND CLAIT E. BRAUN, *Colorado Div. Wildlife, Wildlife Research Center, 317 West Prospect, Fort Collins, Colorado 80526.* (Present address WPG: *Extension Wildlife and Sea Grant, 554 Hutchinson Hall, Univ. California, Davis, California 95616.*) *Accepted 26 Jan. 1980.*

Wilson Bull., 93(1), 1981, pp. 119–121

Reproductive rate and renesting of Red-winged Blackbirds in Minnesota.—Red-winged Blackbirds (*Agelaius phoeniceus*) have an economic impact upon the industry of wild rice (*Zizania aquatica*) cultivation in northern Minnesota (Moulton, J. Wildl. Manage. 43:747–751, 1979). Red-wings nest in the marsh-like, emergent vegetation that borders the peripheral drainage ditches of the wild rice paddies. Very few Red-winged Blackbird studies have provided data on the number of young fledged per female, per territorial male, or per unit area; or on the extent and nature of renesting and movements of females during the nesting season (Dolbeer, Auk 93:343, 1976). The objectives of this study were: (1) to estimate the size and reproductive success of a population of Red-winged Blackbirds on a typical group of wild rice paddies; (2) to estimate fledging rates per male territory and per nesting female; and (3) to estimate the extent of renesting and movement by marked females during the nesting season in this habitat.

The study was conducted from late April to early August 1977 on commercial wild rice paddies (total area 53.2 ha) located 185 km north of Minneapolis, in Aitkin, Minnesota. Nest searching began in early May and continued through July. Active nests (1 or more eggs or nestlings) were checked daily. Prior to nesting, some birds were captured in large mist nets and in a large, walk-in decoy trap baited with oats and live blackbirds. Territorial males were captured in wire traps that used a live, adult male as a decoy (Bray et al., West. Bird Bander 50:4–7, 1975). Nesting females (with nestlings) were captured by placing small pieces of mist net around their nests. Each bird was marked with a USFWS band on 1 leg and a numbered, plasticized-nylon streamer, secured around the tarsus with an aluminum grommet (Arnold and Coon, Bird-Banding 42:49–50, 1971; DeHaven, West. Bird Bander 50:48–50, 1975), on the other leg. Birds were classed as either second-year (SY) or after-second-year (ASY) on the basis of plumage. Females were aged by color of marginal wing coverts (Payne, Univ. California Publ. Zool. 90:57, 1969). An error rate of from 18 (Dolbeer 1976) to 20% (Payne 1969) must be expected when using this technique.

Nesting chronology and success.—A total of 182 nests (154 active) was located and marked along the 9566 m of paddy ditches. Dominant plant species bordering the drainage ditches were broad-leaf cattail (*Typha latifolia*) and narrow-leaf cattail (*T. angustifolia*), sedges (*Carex* spp.), bulrushes (*Scirpus* spp.), various grasses (Gramineae) and some water plantain (*Alisma* spp.) and arrowhead (*Sagittaria* spp.). The first eggs were laid on 17 May and the

Table 1

Nesting and Fledging Rates for 45 Defined Male Territories and for the Entire Study Area

	Male territories	No. of active nests	Min. nesting females	Max. nesting females	Entire study area[a]
	45	120	97	115	53.2[c]
$\bar{x}$ nests or nesting females	—	2.67[b]	2.16[b]	2.56[b]	2.48[d]
$\bar{x}$ young fledged	2.55	0.95	1.2	1.0	2.6

[a] Undetermined number of territories.
[b] Per male territory.
[c] Ha.
[d] Nests per ha.

Table 2

Nesting Parameters for 36 Individually Marked Female Red-winged Blackbirds

	Nesting females	Young fledged/ female	Females renesting	$\bar{x}$ days from end of first nest to start of next nest	Females attempting second brood on area	Renesting females that switched male territories	$\bar{x}$ distance (m) between successive nest-sites[b]
SY females	8 (22)[a]	1.5	2 (33)	7	0	0	—
ASY females	28 (78)	2.04	4 (17)	10	1 (6.6)	3 (75)	169
Total	36	1.93	6 (20)	9.6	1 (5.6)	3 (50)	169

[a] Parenthetical values are percent of total within category.
[b] For the 3 females that switched male territories.

last young fledged on 16 July—a nesting season of 61 days. The median dates for nest starts and fledging were 24 May and 18 June, respectively. The average clutch-size was 3.7 eggs (mode 4). A total of 137 young was fledged from 48 of 154 (31.2%) active nests. Predators, primarily raccoons (*Procyon lotor*), destroyed 99 nests (54.4%). About 80% of all egg mortality and over 50% of all nestling mortality was due to predation.

Territoriality of marked males.—Most males began territorial defense in late April. Of 5 ASY males captured in the walk-in decoy trap and tagged in early May, 2 later established territories on the area. Between 12 and 26 May, 30 ASY males were captured on-territory, in small decoy traps, and tagged. Seven marked males abandoned their territories and were not seen again. Table 1 gives nesting and fledging rates observed on 45 male territories (25 marked and 20 unmarked males). About 2.6 young were fledged per male territory, a low reproductive rate compared to most other studies (Dolbeer 1976). One ASY male abandoned its initial territory and established a second territory 1.4 km away. The first territory contained 1 nest which was depredated with 3 eggs in it on the night of 23–24 May. The second territory contained 1 nest in which the first egg was laid on 6 June and which fledged 3 young on 30 June. The nesting female on the first territory was not marked so it is not known whether or not it moved with the male. Two males in SY plumage successfully defended territories that attracted nesting females. One of the SY-male territories fledged 3 young.

Nesting and renesting by marked females.—Prior to the start of nesting in mid-May, 11 females (5 ASY and 6SY) were captured in large mist nets and marked. Of those, 4 remained on the study area and 3 (2 ASY and 1 SY) nested, but no nest was located for the other SY female. Between 2 and 21 June, 33 nesting females (26 ASY and 7 SY), with nestlings, were captured on their nests and marked. Of the 36 marked females that nested, 8 (22%) were classed as SY birds. The 36 marked females accounted for 42 nests (41 active) on the study area. One SY female built a second nest after the loss of its first nest, but did not lay a second clutch. Table 2 gives values for young fledged per marked female. Of 30 marked females that could have been observed renesting, 6 (20%) renested on the study area. Eighteen marked females successfully fledged young from nests started on or before 3 June. Only 1 marked female successfully produced a second brood on the study area. Three of 6 females that renested switched male territories, moving considerable distances in the process. The phenomenon of territory switching by individually marked, renesting, red-wing females was also observed by Dolbeer (1976) and Fankhauser (Bird-Banding 35:120, 1964). This study and that of Dolbeer (1976) suggest that this kind of movement may be common. Renesting and second-nest values (Table 2) represent minimum estimates since females that left the study

area may have renested elsewhere. Four cases of renesting where clutch-sizes were known for both initial and subsequent nests were observed. In all cases, the females involved were ASY and laid initial clutches of 4 eggs. Only 1 female laid 4 eggs in its second clutch; the other 3 females each laid only 3 eggs in their second clutches.

Acknowledgments.—I thank the C. K. Blandin Foundation and Wild Rice Growers' Association, Inc. for financial support; K. C. Carr and R. S. Wetzel (USFWS) for field support; H. Jacobson for permission to study the rice paddies; and M. W. Weller (University of Minnesota) for reviewing the manuscript. This paper is No. 10401, Scientific Journal Series, University of Minnesota Agricultural Experiment Station, St. Paul, Project 17-92.—Daniel W. Moulton, *Dept. Entomology, Fisheries and Wildlife, Univ. of Minnesota, St. Paul, Minnesota 55108.* (Present address: *70 Edgewood Dr., Central Valley, New York 10917.*) *Accepted 1 Nov. 1979.*

Wilson Bull., 93(1), 1981, pp. 121–124

Migration speeds of three waterfowl species.—To better understand the physical nature of bird migration and its energy requirements, it is important to evaluate the speed at which various species fly, and how speed may be affected by environmental factors. This paper reports on ground and air speed of migrating flocks of Canada Geese (*Branta canadensis interior*), Lesser Snow Geese (*Anser c. caerulescens*) and Mallards (*Anas platyrhynchos*).

In 1966, we began recording ground speeds of migrating waterfowl in central Illinois. By late 1978, we had obtained 160 records, all but 3 from a car driven for 1.5–24 km parallel to the birds' flight. The 3 additional records were obtained from mapping the course and time interval of migrating birds observed from a light aircraft. Migrating flocks of Canada Geese composed 79% of the records, Lesser Snow Geese 16% and Mallards 5% (Table 1).

At the time the waterfowl were observed, the wind direction and velocity were estimated. Direction data were more reliable than velocity estimates, which were based on radio reports and local clues (flag, foliage, smoke and the like). Most flocks were between 100 and 365 m above the ground. At those altitudes, wind direction was approximately the same as at ground level, but average wind velocity was probably higher. The wind force striking the migrating flocks was vectored on the basis of cosine of the angle of wind to migration track × wind velocity.

Table 1 shows the ground speed of the migrants, the vectored air velocity assisting or impeding their passage, the calculated air speed that resulted from the deletion of the wind force and the statistical significance of the results. Data for the Canada Goose were separated into fall and spring periods to determine whether the stronger winds in the spring or the proximity of the wintering grounds were factors affecting the air speed of these geese.

A comparison of ground speed to the vectored wind speed shows that migrating Canada Geese adjusted their flight speed within certain constraints to compensate for wind velocity. Although the ground speeds of Canada and Snow geese flying into the wind were reduced, their effort (as measured by air speed) averaged 13.1 km/h; more when they flew against the wind than when they flew with it. The F value derived from an analysis of variance demonstrated a highly significant relationship between wind speed and the air speed of Canada Geese ($F = 18.5$, $P < 0.01$ for fall and 20.7, $P < 0.01$ for spring), but no statistically significant difference in the Snow Goose ($F = 3.6$, NS). (The small sample measured in the opposed-wind category appears responsible.)

Table 1

The Effect of Vectored Wind Velocity on the Ground Speed of Migrating Flocks of Waterfowl in Central Illinois, 1966–1978

Species	Season	No. of flocks	Ground speed (km/h) $\bar{x} \pm SD$	Wind speed (km/h) $\bar{x} \pm SD$	Corr. coeff.	*P*	Calculated air speed (km/h)
Canada Goose	fall	48	72.7 ± 6.4	+9.3 ± 7.6	0.45	< 0.01	63.4
	fall	26	64.7 ± 9.2	−12.2 ± 9.8	−0.69	< 0.01	76.9
	spring	30	70.3 ± 10.0	+13.0 ± 10.5	0.22	< 0.10	57.3
	spring	22	60.7 ± 6.0	−12.2 ± 7.6	−0.39	< 0.10	72.9
Lesser Snow Goose	fall	21	83.3 ± 5.1	+12.7 ± 6.6	0.17	< 0.10	70.6
	fall	4	67.3 ± 24.0	−13.4 ± 8.8	−0.77	< 0.10	80.7
Mallard	fall	9	71.8 ± 11.1	−18.8 ± 12.2	−0.78	< 0.01	90.6

Within each wind force category (Table 1), linear regression demonstrated change in ground speed with wind speed. As the tail-wind force increased, migrants failed to correspondingly increase their ground speed. The correlation coefficient showed the best linear fit for the Canada Goose fall data. Spring wind data were more variable than fall data, perhaps as a result of a greater frequency of strong gusts at that season. Fig. 1 shows the effect of vectored wind velocity on the ground speed of migrating Canada Geese during the fall and the ground speed that might be expected without adjustment by the geese for wind force. The difference between the actual and projected ground speeds suggests that as favorable winds increase, the birds decrease their air speed and that as head winds increase, they fly faster. Several different plot tests showed that the relationship was linear rather than curvilinear.

The air speed of individual flocks of Canada Geese varied between 25 and 88 km/h. The instance of the highest speed recorded is especially interesting. At 07:15, 10 March 1977, Glen Sanderson and Bellrose were driving north on I-57 at Dix, Jefferson Co., Illinois, when they noticed 500 Canada Geese in 2 flocks migrating due north at an estimated altitude of 300 m. The geese had a ground speed of 96 km/h which they steadily maintained for the next 24 km. Local weather on the car radio indicated a south wind at 8 km/h. These geese had apparently just departed nearby Rend Lake, Jefferson Co., on a flight of about 185 km to a traditional spring concentration point on the Illiniois River near Bureau, Bureau Co.

Because of this high air speed at the apparent onset of a migratory flight, we thought that spring air speeds might be higher than those in the fall because of energy expended on the longer fall flights. Central Illinois is closer to the winter grounds in southern Illinois than to James Bay or even Horicon Marsh, Wisconsin, points from which fall flights through Illinois emanate. However, air speeds of migrants were 4.2 km/h lower in the spring than in the fall ($F = 4.4$, $P < 0.05$). Apparently distance of flight does not appear to be a factor affecting flight effort.

With a following wind in the fall, the air speed of Snow Geese was 7.2 km/h greater ($P < 0.01$) than that of Canada Geese. The difference was significant ($F = 12.0$, $P < 0.01$). Flying against the wind in the fall, Mallard air speed also averaged 13.7 km/h faster than Canada Geese ($F = 21.4$, $P < 0.01$).

There is conflicting evidence regarding the effect of wind speed on the air speed of migrating birds. Blokpoel (Can. Wildl. Serv. Rept. Ser. 28:1–30, 1974) compared a small num-

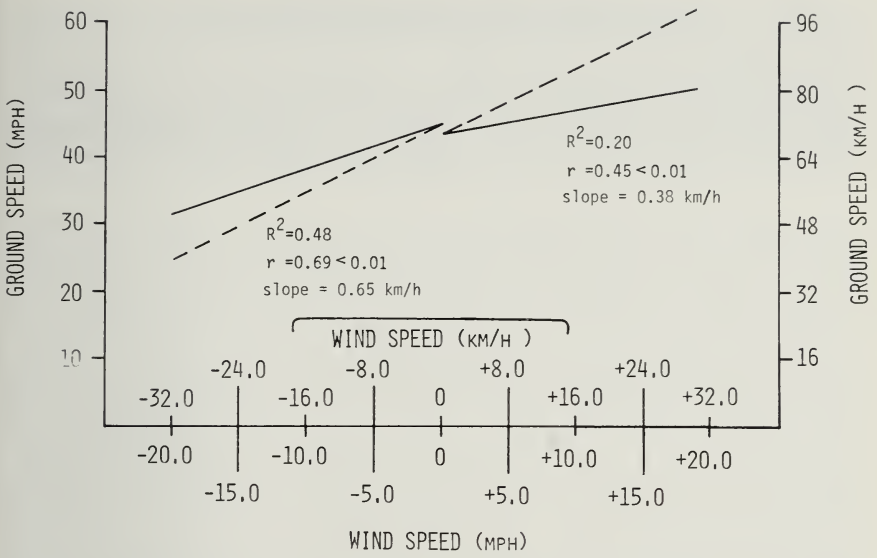


FIG. 1. Linear regression of the response of Canada Geese in ground speed to favorable wind speed and adverse wind speed. Dashed line indicates projected ground speed with no change in air speed.

ber of air speeds with wind speed records for migrating Lesser Snow Geese and concluded that wind speed resulted in little, if any, change in the air speed. Although Tucker and Schmidt-Koenig (Auk 88:97–107, 1971) found that air speeds of local birds varied with the component of the wind (head, tail or cross), they minimized the importance of energy conservation resulting from a bird altering its air speed, stating: "The air speeds we measured are too variable to support the hypothesis that birds fly at closely regulated air speeds to conserve energy."

On the other hand, Schnell (Living Bird 4:79–87, 1965) measured the local flight speeds of birds near the ground by Doppler radar and found that wind velocity affected the air speed of most birds. Bellrose (pp. 281–309 *in* Proc. XIV Int. Ornithol. Congr., 1967) noted that the speed of bird migrants on radar was not proportional to increases in wind speed, and suggested that migrants adjust their energy output in relation to the degree of wind assistance or resistance. Bruderer and Steidinger (pp. 223–258 *in* Animal Orientation and Navigation, S. R. Galler et al., eds., SP-262, U.S. Gov't. Print Off., Washington, D.C., 1972) used radar to ascertain that ground speeds of Chaffinches (*Fringilla coelebs*) in migration did not parallel increases in wind velocity; their decrease in air speed equalled about one-third the increase in wind force. In a further study of the flight speeds of 12 species of gulls (*Larus* sp.), terns (*Sterna* sp.) and skimmers (*Rynchops* sp.) near their nesting colonies, Schnell and Hellack (Am. Nat. 113:53–66, 1979) obtained additional evidence that bird air speeds usually varied inversely to wind speeds. Additional work by Tucker (pp. 298–333 *in* Avian Energetics, R. A. Paynter, Jr., ed., Publ. Nutt. Ornithol. Club No. 15, 1974) apparently led him to modify his views on the energy expended in flight: "At both sea level and altitudes of 6000 m, it is beneficial from an energetic point of view to fly faster into a head wind, and slower with a tail wind than is the case in still air."

Varying results obtained when comparing air speed of birds with wind speed may be a function of the wide range of air speeds that birds can use without the undue loss of energy. Schnell and Hellack (1979) concluded that ". . . air speeds can be increased or decreased considerably with only a relatively small increase in metabolic rate or cost of transport." As shown by Greenewalt (Trans. Am. Philos. Soc. 65:1–67, 1975) cost of transport curves are relatively flat near their minima.—Frank C. Bellrose and Robert C. Crompton, *Illinois Natural History Survey, Havana, Illinois 62644.* *Accepted 19 Dec. 1979.*

Wilson Bull., 93(1), 1981, pp. 125–134

ORNITHOLOGICAL LITERATURE

Two divergent reviews of the following title, Nomina Anatomica Avium: an Annotated Anatomical Dictionary of Birds, have been received by the Editor. Both are published for the benefit of the readers.

NOMINA ANATOMICA AVIUM: AN ANNOTATED ANATOMICAL DICTIONARY OF BIRDS. By J. J. Baumel, A. S. King, A. M. Lucas, J. E. Breazile and H. E. Evans, (eds.), with R. L. Zusi (consultant for taxonomy) and L. Malinovský (consultant for classical languages). Academic Press, London and New York, 1979:xxv + 637 pp. $64.50.—The study of avian anatomy is pursued by workers in a variety of fields including systematics, neurobiology, veterinary medicine, physiology, poultry science and others. Communication between workers in different areas, and even in the same area, has long been hampered by the lack of a universal system of names for the parts of the avian body. This problem has now been remedied by the publication of the Nomina Anatomica Avium (NAA) after a decade of work by the approximately 80 scientists constituting the International Committee on Avian Anatomical Nomenclature. The purpose of NAA is to provide a list of terms for the parts of the avian body, and thereby to advance the anatomical study of birds. Subcommittees dealing with the different body systems attempted to minimize changes in well-established terms while providing for each structure a single term that is short, easy to remember and informative. Topographically related structures are given similar names, and eponyms are avoided. The nomenclature is in Latin for the sake of international communication.

The book opens with a brief history of the project and information on the use of the NAA, followed by a series of chapters dealing with the individual organ systems. Few readers will make use of the whole book, but workers who study avian anatomy for any reason should find one or more chapters dealing with organ systems relevant to their investigations, and which will provide them with a standardized terminology for use in publication and other technical communications. The book is much more than just a collection of terms, however. It is extensively illustrated with labeled drawings of various anatomical structures, some of them taken from published research reports, but many of them newly drawn for this volume. The lists of terms are heavily annotated with explanations of the reasons for the choice of terms, homologies, synonyms and variations in different groups of birds. There is an extensive list of references establishing the authority for the decisions made in the choice of terms, and a lengthy index to the terms themselves and their major synonyms. The content of the book is accurately described by its subtitle.

The ultimate success of this venture will depend upon the extent to which the NAA nomenclature is adopted by researchers and writers. If the ideal of a unified nomenclature is to be achieved, it will be necessary for virtually all workers to use the system in their publications, even when it differs significantly from that to which they are accustomed. This may pose some temporary inconvenience but should be beneficial in the long run. Most investigators will probably find that the new nomenclature is not radically different from older ones because changes were not made for the sake of novelty but only to introduce clarity and eliminate confusion. Nevertheless, there will be some workers who will find themselves unwilling to adopt the NAA nomenclature. In such cases it would be useful to provide a table correlating the terms used with their NAA counterparts. If the reason for reluctance to adopt NAA terms is substantive then I recommend strongly that the individual communicate with the appropriate subcommittee chairman (listed in the book) and explain the objections to the NAA terms. If the reasons for rejection are sufficiently compelling, it

may be possible to change them in a future edition of the NAA. Workers whose investigations reveal new variations in anatomical structure, or who discover that the current terminology is based on incorrect or inadequate information should also communicate their discoveries by sending reprints or comments to the appropriate subcommittee chairman. The first edition of NAA is not intended to be the final word on avian anatomical nomenclature. It is intended that revised editions will be prepared in future years so that the work will increase in effectiveness as a basis for communication among avian anatomists.—Robert J. Raikow.

Nomina Anatomica Avium: an Annotated Anatomical Dictionary of Birds. A second review.—The Nomina Anatomica Avium (NAA) is an ambitious work, necessitated by the nomenclaturally confusing mosaic of over- and under-represented areas confronting avian morphologists. Eighty contributors labored for more than a decade to produce the NAA, taking as their objectives the "promotion of international communication by establishing an agreed list of terms in a universally acceptable language" and "the advancement of anatomical knowledge of birds." If these intentions had been met the NAA would indeed be a pearl beyond price and justify the claim on the flyleaf that "it is an essential work of reference for all avian scientists and every zoological library." Unfortunately, neither objective has been completely fulfilled and while many sections are excellent, the resultant hybrid may be problematical enough to dissuade ornithologists from perusing subsequent editions or following current recommendations.

There is no question that communication is enhanced by nomenclatural stability, so any work, such as the NAA, that attempts to provide the framework for standardization is to be commended. However, if stability is to be maintained in derivative studies, it is imperative that the syntax of the terminology be intelligible, and this is a facet of standardization for which little provision has been made in the NAA. In common with other anatomical reference works (e.g., Nomina Anatomica Veterinaria, Jena Nomina Anatomica, etc.), Latin was the nomenclatural source chosen by the International Committee on Avian Anatomical Nomenclature (ICAAN) for the NAA.

The fact that most ornithologists (including anatomists, who tend to work in their own vernacular) are unfamiliar with the language was recognized in the introduction to the NAA, where it was suggested nevertheless that "the Nomina should not be neglected simply because of the unfamiliarity of Latin. It bears repeating that the official Latin terms should be used in scientific articles and books in order to enhance international scientific communication." It may also reasonably be argued that many researchers are already familiar with the vernacularized Latin of textbooks and that attempts have been made in the NAA to provide some Latin equivalents at least suggestive of the terms already used in the Romance languages and English. However, textbook Latin is hardly adequate preparation for the nomenclature of the NAA, where nouns and associated adjectives mostly exhibit the number, gender and case of the unadulterated forms. To ornithologists with little or no formal knowledge of the language, the rules which distinguish Os palatinum (palatine bone), Processus palatinus (palatine process) and Facies articularis palatina (surface which articulates with the palatine) are not clear. In addition, those unfamiliar with the manner in which word stems affect the declension of a noun would be hard pressed to recreate the procedure which derives a nominative plural of tractus from Tractus but musculi from Musculus. As the list of terms given in the NAA is deliberately not exhaustive, the potential for a new era of nomenclatural confusion in subsequent studies is obvious. The remedy for this difficulty is simple enough, and it is hard to rationalize the absence (in a work already comprising 637 pages) of a short appendix which comprehensively lists plural and adjectival forms and which explains the syntax of the present terminology clearly enough to serve as a guide for future

use. Criticism of the NAA for failure to provide a Latin grammar, however brief, should not be dismissed as yet another example of pedantic nit-picking. Haphazard or arbitrary 'Latinization' of terms by ornithologists anxious to comply with NAA principles, but unable to locate appropriate sources or to deduce suitable terms from questionable analogues will promote neither communication nor standardization.

The second intent, that of advancing anatomical knowledge of birds, suffers from the same theme of critical omission as the first objective. The NAA is subtitled 'an annotated anatomical dictionary of birds' giving the misleading impression that the annotations are supplemental to the regular dictionary format of comprehensive definition. Although there is some variation (for example, the chapter on the respiratory system is comprehensively annotated and illustrated), in general the list of terms which prefaces each chapter is incompletely annotated, and even fewer structures are figured. As a result, many features are both undescribed and unillustrated. The practice of differential annotation is easily justified when a system of nomenclature has stabilized sufficiently that some terms require no further definition. It is an inappropriate principle for any study that attempts to be the definitive work within a discipline, especially if the raison d'être for that study has been long-standing nomenclatural confusion. Non-morphologically oriented ornithologists seeking, for example, to extend their knowledge of the oral cavity will find the listing of terms such as Radix linguae or Fenulum lingualis less than informative in the absence of further description. The dictionaries (Donath and Crawford 1969, Kenneth 1966) cited in the introduction as useful in the development (in the sense of etymology, not syntax) of Latin terms, are limited in the extent to which they may be used to supplement the NAA. Many terms (e.g., Ovogonium, Polocytus secundarius) undescribed and unfigured in the NAA are similarly absent in the references mentioned. In addition, the dictionary by Donath and Crawford is pertinent to human, not avian, anatomy and there are often radical differences in the meaning of similar terms. For example, the principal aortic vessel in birds is derived from the right member of the embryonic fourth pair of aortic arches while the principal vessel in mammals is the left member of the fourth pair. Extreme caution is therefore required in extrapolating explanations from other dictionaries to undefined terms of the NAA.

Differential annotation is equally problematical for avian anatomists familiar only with the vernacular terms of their specialties. As the index is exclusively in Latin and as vernacular synonyms are generally (though again, variably) lacking in the text, a dubious combination of translation and elimination is required to match undescribed Latin terms with their vernacular equivalents. Anatomical knowledge of birds seems hardly likely to be advanced while ornithologists are unable to readily locate or identify features of interest. Exhaustive annotation and a vernacular index would do much to eliminate these problems.

Quite apart from the difficulties described above, the NAA contains a number of inconsistencies, errors and ambiguities, illustrated by the following examples. In the chapter on muscles, the term 'Pars' (to denote a distinct and consistent subdivision of a muscle) is capitalized throughout the list of terms, whereas the lower case is used throughout the annotations; in the list of terms the muscles of the jaw are referred to Figs. 2 and 3, which in fact illustrate the muscles of the hyoid apparatus and tongue, and Musculus pectoralis is used both to indicate an entire muscle (said to comprise 3 parts: pars subcutanea thoracica, pars subcutanea abdominalis and pars propatagialis) and, in Figs. 5 and 6, a prominent, previously unidentified, subdivision (? M. pectoralis pars thoracicus, sensu George and Berger 1966) ventrocaudal to the M. pectoralis pars propatagialis. Other examples abound: the Lamina parabasisphenoidalis (p. 90, annotation 98) was previously referred to as the Lamina basiparasphenoidalis (p. 89, annotation 96) while the Tuba pharyngotympanica communis (p. 89, annotation 94) is shortened to Tuba pharyngotympanica on p. 90 (annotation 98); the Canalis olfactorius and Palatum are not on the pages (108 and 282, respectively) cited in the

index; the Rostrum sphenoidale is missing from Fig. 1 of the osteology section, in contrast to the reference given in the list of terms, and although Musculus subscapularis is described, no corresponding description is given of Musculus subcoracoideus. The list could be extended, but the examples given are sufficient to demonstrate that the NAA could have benefited from more careful proof-reading.

Despite these difficulties, there is valuable information to be gleaned from the NAA by those ornithologists willing to brave the problems imposed by the format. The notes appended to the chapter on the respiratory system, for example, are models of informed comment unimpeded by jargon, while critical analysis of the literature in the light of new (often previously unpublished) information elevates many other annotations from the realm of simple description. Many of the illustrations throughout the book are superb, although it must be admitted that others (e.g., Fig. 1) seem more likely to amuse than enlighten. Finally, more than 900 citations in the bibliography ensure adequate extension of the anatomical foundation laid by the text, regardless of the area of specialty. Given that the problems previously described can be resolved, the excellence of much of the text and many of the figures indicates the potential of subsequent editions of the NAA for meeting the objectives of the current contributors. For the present, let the buyer beware.—R. Johnson.

Donath, T. and G. N. C. Crawford. 1969. Anatomical dictionary with nomenclatures and explanatory notes. 1st English Edition. Pergamon Press, London, England.

George, J. C. and A. J. Berger. 1966. Avian Myology. Academic Press, New York, New York.

Kenneth, J. H. 1966. Henderson's dictionary of biological terms. 8th Edition. Van Nostrand, New York, New York.

British Birds—A Field Guide. By Alan J. Richards. David & Charles Ltd., North Pomfret, Vermont, 1979:192pp., 186 color photographs, 186 line drawings. $14.00. — This is an attractive book in many ways. Well produced, with good illustrations, clear type on good paper, and a sturdy binding, it is a pleasure to thumb through. It contains species accounts of 186 British birds, one to a page, each with a color photograph and a line drawing. The photographs are of excellent quality and accurately reproduced; the adequate, if not inspiring drawings by Rob Hume supplement the photographs by showing the birds in flight or in different plumages or poses. The species accounts are divided into five sections: characteristics, voice, habitat, nest and status. Under "characteristics" are included a description, often rather abbreviated, and notes on locomotion, behavior, food, roosting and other points of general interest. Under "status" are included population figures for each species, taken from Sharrock's Atlas of Breeding Birds in Britain and Ireland (1976). This is a useful feature for the layman who may not have access to the Atlas. Some species accounts have a sixth section, "similar or allied species," where some of the more common British birds not among the favored 186 are briefly described.

As far as it goes, this is a worthwhile book. But how far does it go? For an ornithologist or a keen birder, not nearly far enough. The British list contains ca. 475 species, of which some 270–290 occur every year. A great many have been left out of this book, thus rendering it useless to the person who wants to identify every bird he sees. According to the very skimpy introduction, the book is aimed at "those thousands of people interested in the birds in their gardens and local parks, in the countryside or on the moors . . . " etc.; in other words, the armchair or junior-intermediate birder who has perhaps graduated from the bunny slopes but is not yet ready for the advanced runs. The 186 species treated are described as

"those which might be seen in Britain without too much effort over the course of a year," although the choice sometimes favors distinctive or photogenic species over those less well endowed. The drab Rock Pipit (50,000 breeding pairs) only appears under "similar or allied species," whereas the Dotterel (100 pairs), Red Kite (30 pairs) and Osprey (several pairs) are accorded full treatment.

In spite of its title, this is only a partial field guide to British birds, and it will certainly not replace any of the existing works. It is a book for the educated layman. My advice to readers of The Wilson Bulletin is: if someone gives it to you for Christmas, accept and enjoy; but don't spend hard-earned money adding it to your library.—Stuart Keith.

Hawks and Owls of North America. By Donald S. Heintzelman. Universe Books, New York, New York, 1979:197 pp., 68 photographs (8 color), 4 figs., 1 table. $18.50.—While the title of this book recalls the excellent but out-of-print classic Hawks of North America by Dr. John B. May, and its successor North American Birds of Prey by Alexander Sprunt, Jr., the present book is less a systematic treatment than a more popular book addressed, in the author's words, "to raptor enthusiasts at less than the professional level." Its chief feature is its display of photographs, some in color, of most of our raptors. The informal text of discursive, rather than ordered systematic accounts, is a vehicle to show more of the rapidly-growing files of hawk photographs. Many of these are excellent (but that of a disheveled captive White Gyrfalcon is not). Some half of these photographs are by the author, but the rest are by many different photographers. The author acknowledges his debt to many sources, but for the most part there is little to indicate sources of information. (Who supplied the information about the subspecies of Black Hawk which lives "in southern Florida"?)

There are separate chapters on vultures, kites, accipiters, soaring hawks, etc., and the individual species are afforded a variable selection of information and comment, but I find little here to commend it to other than the general reader. The species accounts are followed by chapters on matters of current interest, such as endangered species, habitat loss, ecology (an over-worked term in this text), migration, conservation and chemical pollution.

At recent meetings of Raptor Research, the number of attending raptor enthusiasts doubled that of A.O.U. and Wilson Society meetings. Many of these have seemingly little other contact with wildlife biology, but my acquaintance with them leads me to believe they are more sophisticated than the audience to which this book is addressed. It seems unfortunate that we in North America do not have a volume in any way comparable to Leslie Brown's superb British Birds of Prey.—Walter R. Spofford.

The Peregrine Falcon in Greenland: Observing an Endangered Species. By James T. Harris. University of Missouri Press, Columbia and London, 1979:255 pp., 39 plates, 1 map. $15.95.—This is neither a scientific treatise nor the definitive monograph on Greenland's Peregrine Falcons (*Falco peregrinus*). A "narrative of a summer's research in Greenland," it is much more than an ordinary diary. Harris has written an unusual and fascinating book that should be a must for all collectors of good bird books.

The title and subtitle should be reversed, as the book deals more with the adventure of observing falcon cliffs, their birds and their weather than with the Peregrine Falcon in Greenland. Thus, at first glance, I was disappointed: I expected graphs, tables and statistics. Many of these data are included, woven skillfully into the personal narrative of the Greenland

experience of 1972. It is difficult, however, to find them quickly: the index is short and emphasizes the work of other authors rather than Harris' own observations. Apart from these slight disappointments for the raptor expert there is much to admire in this handsome book, and we must congratulate the publisher for an excellent and esthetic production. The cover design (by Jerry Dadds), the selection of black-and-white photographs and even the italic print of the whole book enhance the author's objectives and style. Harris attempts to blend three different stories together: the search for falcon eyries (partly a travelogue and diary), the observations of falcon activities and behaviors at one eyrie (the proper topic of the book) and "the development of my feelings toward the species and the individual falcon" (the most difficult part to write).

The book serves as an excellent introduction to the tundra ecosystem and to the care and preparation that must go into such a wilderness study. Thus, I recommend it highly as background reading for anyone bound for the Arctic. Songbirds, mammals and other raptors are not only described but also followed through the seasonal cycle as long as they occur within the "falconscape."

The peregrine story is two-fold. The author makes an admirable attempt to provide extensive background notes on the species. He begins by recounting the general population decline and its inter-relationship with the use of pesticides, then introduces the species and subspecies concepts, and talks about distribution, population surveys and other topics. Finally, we learn about captive breeding at Cornell up to 1977, and the latest breeding data for Greenland. These sections come somewhat abruptly and distract from the ongoing narrative. Yet, for most readers, Harris has written an excellent summary of the complex peregrine problem.

The account of breeding activities is rather general and contains only the occasional "bonbon" for the specialist, e.g., the observation of "hop hunting" Lapland Longspurs (*Calcarius lapponicus*) on the ground. This is not mentioned in the index. The interested reader must go to various journals where scientific papers by some of Harris' companions have been published in the meantime. Thus, the jacket's promise, "Harris' reporting is a model of scientific accuracy," is certainly exaggerated. Today, the term scientific accuracy should mean more than occasional behavioral anecdotes.

Finally, the most difficult part of this review, an evaluation of Harris' feelings and his writing about them. Everyone who has watched birds in the wilderness will share some of the conscious and unconscious thoughts and moods that he felt sitting day after day amidst flowers and mosquitos. Occasionally, however, he slips into metaphors and statements too grandiose for this context. Examples are: "A sense of kinship had crept upon me, a feeling that we shared the difficulty of living, and their presence, their successes, even the humming of mosquitoes, encouraged me." (p. 63); "The mammals and I seemed to share an immediate recognition. An illusion took hold of me, that we had a mutual understanding of and interest in our parallel lives, because we all had fur or four-chambered hearts or some bond." (p. 64); "Most oologists alive today are aging retired men with rich memories." (p. 85); "Almost always humans are individuals. Animals are not." (p. 193).

There are many dialogues in this book that do not sound at all like field ornithologists talking in the field. They are too clean, too literate compared to my experience of many years. This introduces some element of artificiality, and quite a bit of distance from such writers as Matthiessen and Abbey, to whom Harris is compared on the book jacket. Still, we learn quite a bit about the author. He immerses himself in the tundra wilderness, becomes extremely protective of the falcons, and finds himself ill at ease with the sudden appearance of human visitors. Harris—in one of the best dialogue areas of the book—is caught breathlessly almost stunned by the sudden confrontation with another world, and escapes back into the tundra night.

This beautifully produced book is a successful and rare (albeit not perfect) blend of ornithological adventure, scientific information and personal touch. It is well worth its price.—HARTMUT WALTER.

SHOREBIRDS IN MARINE ENVIRONMENTS. By Frank A. Pitelka (ed.). Studies in Avian Biology, No. 2, Cooper Ornithological Society, 1979:261 pp., 70 figs., 52 tables. $8.00.—This volume is a collection of papers from a symposium on shorebirds held at the 1977 meeting of the Pacific Seabird Group. The symposium, organized by F. Pitelka, was composed of two sessions: one on distribution, migration and conservation (15 papers); and the other on ecology of shorebirds (5 papers, 4 abstracts). The objectives of the symposium were to look at distribution, migration and ecology of shorebirds in terms of the basic information currently available, and to examine shorebird biology in terms of the conservation and management of coastal wetlands. Pitelka sets the stage for the discussion by examining shorebird distribution on the Pacific Coast. Such a larger view of an entire coast is essential since shorebirds are long-distance migrants. Pitelka lists the new world shorebirds, and comments on their status on the Pacific Coast. He then analyzes the world shorebird fauna (fig. 1). One particularly helpful figure shows the occurrence by five degree latitude intervals of shorebird species in North and South America. He briefly outlines the current problems in shorebird distribution: the importance and occurrence of staging areas, migration behavior (group dynamics), age and sex differences in patterns, and winter site tenacity. His introduction is an excellent starting point for the collection of papers, and for graduate students interested in shorebirds.

The papers on distribution, migration and conservation cover a wide range of topics including censuses of restricted areas and wide-ranging areas, habitat use, timing of migration, migration patterns of particular species and the evaluation and conservation of coastal wetlands. Some papers merely report on census techniques; illustrating the kinds of information available from large-scale censuses (see Prater), or in-depth censuses of small bays (see Gerstenberg). Other papers illustrate the importance of particular bays for migrating shorebirds. The Copper River Delta is a critical habitat for migrating shorebirds as some 20 million shorebirds pass through this area each spring (see Isleib). The delta is particularly important to species such as Western Sandpiper (*Calidris mauri*) and Dunlin (*C. alpina*) that forage there and lay down fat reserves for continued northward migration (Senner). Senner found that Dunlin migrate collectively, shift from one place to another as flocks, and show greater weight gain than do Western Sandpipers that migrate independently of each other in less organized flocks while in the Copper River Delta. The information provided by Senner is critical to protecting these areas against human activities (such as oil spills). Similarly, Gill and Jorgensen present quantitative data on shorebirds' use of another Alaskan bay.

The paper by Page et al. is an excellent example of the information that can be gained by censuses for many years. The mass of data fall into species patterns, and provide insights into habitat requirements and site tenacity. Many species returned to the same foraging areas year after year. Winter feeding site fidelity was also found by Smith and Stiles, who banded shorebirds in 2.5 years at a mudflat in Costa Rica.

Two excellent papers on migration patterns deserve special mention: Jehl's on the autumnal migration of Baird's Sandpiper (*C. bairdii*), and Harrington and Morrison's on migration of Semipalmated Sandpiper (*C. pusilla*). Jehl's is an innovative examination of the migration pattern of Baird's Sandpiper using specimens from 35 museum and university collections (if I count the acknowledgments correctly!). The project involved a good deal of work and imagination, and the end results of the country-wide survey indicate sexual and age differences in the migration pattern of this species. Adults may migrate some 9000 miles in 5

weeks, whereas juveniles migrate more leisurely over a broad front (Jehl). Although I would have liked to know exactly how many specimens were examined, the paper illustrates how museum specimens can be used to answer ecological questions.

Harrington and Morrison's paper on the Semipalmated Sandpiper uses a variety of techniques (banding studies at James Bay and Massachusetts, and examinations of museum specimens) to show that different populations have different morphological characteristics that allow for identification of the source of migrants. The paper clearly indicates that a variety of strategies are employed by one species while migrating. Their migration pattern is a very complex system in which breeders from different geographical areas use different routes and their patterns vary seasonally. Such large-scale, cooperative studies can provide information necessary for an overview of migration and habitat use that is simply not possible by individual investigators working by themselves in one bay.

Two other papers in this section (Speth, Goss-Custard) comment on the management of wetlands, and the effects of habitat loss on overwintering shorebirds. The paper by Goss-Custard is excellent in that it makes predictions about the food base of shorebirds, and provides data relevant to them. Jehl's concluding remarks are concise and point out topics requiring extensive work.

The second part of the book deals with the ecology of shorebirds and includes papers on flocking behavior, winter and summer ecology, feeding ecology, energetics, and territoriality of wintering shorebirds. This section is mainly papers on particular research topics with one or a few species. As such, the papers are excellent, and provide good reviews of topics, quantitative data, and fruitful discussions. The inclusion of the abstracts was frustrating, as I wished to see the entire papers.

Strauch and Abele's paper on feeding ecology of plovers wintering in Panama was particularly interesting in illustrating that some species feed only at low tide whereas others are tidally independent. The study by Myers, Connors and Pitelka on territoriality in non-breeding shorebirds is a landmark study showing that a wide variety of species will defend territories during the winter, although its expression differs among species, individuals and habitats. These data suggest that extensive cost-benefit analysis of foraging may lead to more quantitative predictions of the point at which particular species will stop defending territories. Goss-Custard's analysis of the energetics of foraging Redshanks (*Tringa totanus*) is an excellent example of an examination of these cost-benefit considerations. J. Wiens' concluding remarks point out some of the areas that need further research, making a plea for long-term studies.

Altogether this volume is essential for all ornithologists, particularly those working with shorebirds, migration patterns, foraging behavior, territoriality, habitat selection and conservation. Although papers vary from brief essays without quantitative data, to hypothesis-testing and data-based papers, the overall quality is excellent. The papers provide documentation on several important aspects of shorebird biology (i.e., age and sex differences in migration patterns, site tenacity during the winter, winter territoriality). In the very least they provide quantitative data on migration patterns essential to understanding the importance of coastal wetlands. I was disappointed in the lack of any papers on non-Pacific coast areas (except for Harrington and Morrison). Although it would have taken a lot of time, an index would have made this volume more useful for beginning graduate students or others interested in tracing particular ideas (for example, feeding site tenacity over the winter). Similarly, the volume was a long time in coming out, which resulted in some key papers not being cited. All in all, I cannot recommend this volume more highly. And for $8.00, it's clearly the bargain of the year.—JOANNA BURGER.

A Field Guide to Western Birds' Nests. By Hal H. Harrison, illus. by the author unless otherwise credited; map, endpapers and logo by Mada Harrison. Houghton Mifflin Company, Boston, 1979:xxx + 279 pp., 32 color plates with captions, 153 black-and-white photographs, 1 map, glossary. $11.95 (hard cover).—Here is another attractive addition to The Peterson Field Guide Series—the eagerly awaited companion volume to Hal Harrison's 1975 A Field Guide to Birds' Nests of 285 species found breeding in the United States east of the Mississippi River. The latest work represents a more exhaustive review of the literature than the earlier one; included are all species, even the casual or rare ones, known to breed in the contiguous United States west of the Mississippi River. For nearly each of the 520 species there is a succinct description of its breeding range, habitat, nest, eggs and other pertinent notes. This handy pocket-sized book is packed full of practical information that I am already putting to good use.

The color illustrations are excellent despite their tiny size (only 40 × 53 mm). The nests centered in the 256 color photographs are so graphically portrayed that one can identify many of them without using the captions; the same can be said of the eggs whose markings and colors for the most part are clearly defined and lifelike. The eggs especially are so well illustrated and described that one wonders why the author failed to include them in the book's title. However well done, I find it somewhat disappointing to look at photographs of nests situated in artificial nest boxes, but so many birds these days raise broods in human-contrived sites that the author logically illustrated a number of them. If that unavoidable little problem over natural vs artificial sites disturbed me, I find it hard to fault the numerous black-and-white photos—all of very high quality and nicely placed throughout the text.

Harrison's use of the Mississippi as a boundary between east and west—a method devised earlier by Olin Sewall Pettingill, Jr.—seems to work well. Inasmuch as I spend a fair share of my time on the upper Mississippi, I can vouch for Harrison's accuracy for this region. I also note that he left few stones unturned in other areas of the country familiar to me, e.g., Kansas with its many unusual records, including that remarkable Harris' Hawk (*Parabutea unicinctus*) nesting far beyond the species' usual breeding range. The few places where I find omissions in the text are readily referrable to unpublished material—hardly the fault of the author! By and large, Harrison's careful coverage of the huge block of 22 states appears to be nothing less than outstanding.

One is impressed by the fact that nearly all of the photographs were taken by the author. Only those who know how difficult it is to find the nests of a good many of our birds will appreciate Harrison's special talents, perseverance and endurance. I personally have seen so few nesting birds west of the Rocky Mountains that I hope to spend my retirement days chasing them down in the far west. One reliable reference that will accompany me will be this western guide.—David F. Parmelee.

North American Ducks, Geese and Swans. By Donald S. Heintzelman. Winchester Press, New York, New York, 1978:xiv + 236 pp., color and black-and-white photographs, wildlife refuge maps. $15.00.—A Guide to North American Waterfowl. By Paul A. Johnsgard. Indiana Univ. Press, Bloomington and London, 1979:274 pp., color plates, black-and-white drawings, range maps. $15.95.

In these volumes we have a mixed bag of information concerning the waterfowl of North America. One offers an invariably sparse treatment of field recognition, size, flight habits and ranges in North America, and the second a relatively complete coverage of each species

(food habits, range maps, behavior, etc.). Both books contain numerous photographs of varying quality.

Heintzelman states his purpose as helping hunters and birders to identify waterfowl and to highlight selected national and state wildlife refuges where waterfowl are prominent. The species accounts are brief and general with most of the limited text devoted to field recognition. Habitat for the Gadwall (*Anas strepera*) is "ponds, lakes, rivers, freshwater marshes" and its North American range described as "southern Canada and the United States." I doubt that the comments under the rubric "flight style" (e.g., "direct and rapid," "graceful and rapid," etc.) will really be of much aid to even novice observers. The photographs accompanying the species accounts are black-and-white, and average in quality, but a selection of better quality color photographs graces the book's centerfold. The author employs a taxonomic scheme of subfamilies that is generally outdated in usage (e.g., Aythyinae) but otherwise has presented current nomenclature for the species.

A naive chapter devoted to "Techniques of Waterfowl Study" tells us that "a pair of binoculars is very helpful to people looking at waterfowl," mentions that telescopes are also useful ("a minimum magnification of 20× is necessary"), notes that blinds are also helpful, since hunters have long used them, and sketches the vicissitudes of common and scientific names and "the species problem." Subsequent chapters briefly—some are scarcely more than two pages in length—describe eclipse plumages and hybrids, migrations (with flyway maps), prairie pothole breeding grounds and local viewing areas. The final chapter is more extensive, and presents maps and succinct descriptions of waterfowl refuges in the U.S. Four appendices treat accidental sightings, Canadian wildlife areas, conservation organizations and homes for Wood Ducks (*Aix sponsa*).

The book contains some errors (e.g., Hockbaum for Hochbaum in the suggested reading section) and poor layout in some places (e.g., the figure on p. 226 describing construction of predator guards for Wood Duck nest boxes has no caption or cross-reference with the associated text on p. 220). On balance, this is not a book for ornithologists and, considering the competition available, it may be of marginal value (at $15.00) to anyone.

Johnsgard's prolific pen adds yet another waterfowl book to his long list of credits. To be sure, this is a shortened version of his treastise Waterfowl of North America (1978), as the author freely admits. The range maps and "in hand," "in field" identification sections are unchanged for the most part, whereas a "natural history" section condenses the more detailed material appearing in the earlier volume. The condensed text remains a useful reference to habitat, foods, behavior, breeding and conservation for each species, but without extensive literature citations. Most species accounts are accompanied, however, by at least one suggested reading and, while some of these may be overly general or indeed quite narrow, it is not easy to assign a single reference or two with equal coverage for the likes of a Mallard (*Anas platyrhynchos*) or, conversely, a Steller's Eider (*Polysticta stelleri*).

The color plates are largely the same as appeared before but some new drawings (the author's) are included. Sketches of head profiles (where plate numbers are missing but the sketches are cross-referenced with a numbered species list) are new and supplement the dichotomous key repeated from the 1978 volume.

Johnsgard intended this volume to reach the "middle ground" of his reading audience, those whose needs lie between heavier works and a simple field guide. Perhaps one might have wished for a slightly smaller-sized book, with soft cover, to make it more field-worthy, but I believe Paul Johnsgard adequately has met his goal, and I can recommend the book, as is, for its stated purpose.—Eric G. Bolen.

Wilson Bull., 93(1), 1981, pp. 135–136

ORNITHOLOGICAL NEWS

ANNUAL MEETING—THE WILSON ORNITHOLOGICAL SOCIETY, 1981

The 62nd annual meeting of The Wilson Ornithological Society will be held on the campus of Mount Allison University, Sackville, New Brunswick, Canada, 4–7 June 1981. This will be only the second Wilson Ornithological Society meeting to be held in Canada, and the only one to feature excursions in 3 provinces. The Maritimes feature small towns and largely undeveloped surroundings, with a leisurely pace of life that should provide a relaxing change.

The meeting will be hosted by the Canadian Wildlife Service—Atlantic Region, Mount Allison University, and the Chignecto Naturalists Club. Information concerning accommodations, transportation, excursions and related matters, and a call for papers will be mailed to the society membership in early March 1981. The deadline for submission of abstracts is 15 April 1981.

Chairman of the local arrangements committee is Anthony J. Erskine, Canadian Wildlife Service, P.O. Box 1590, Sackville, New Brunswick, Canada E0A 3C0. Chairman of the program committee is Jerome A. Jackson, Department of Biological Sciences, P.O. Drawer GY, Mississippi State University, Mississippi State, Mississippi 39762 U.S.A.

EDITOR'S ACKNOWLEDGMENTS

The processing of manuscripts received by The Wilson Bulletin during 1980 was greatly facilitated by careful evaluations by more than 75 persons who served as referees. I and the rest of the editorial staff are most grateful to them for their constructive criticism on behalf of our contributing authors. I also thank all authors for their courteous cooperation with our staff as we work together to produce the best papers, both with respect to scientific content and quality writing. The regular editorial staff and others who provided assistance in 1980 were: Dave Ankney, Melinda Barlow, Tim Barlow, Keith Bildstein, Gary Bortolotti, David Brooks, Ann Crabtree, Brete Griffin, Rosemary Johnson, Dot Richardson, Jim Rising, Richard Snell, Pat Urquahart and especially Margaret May and Nancy Flood. We also appreciate the fine efforts in our behalf from the staff at Allen Press, who direct their best energy to our journal. Thanks also for support from Jerry Jackson, Ken Parkes, Bob Storer and George Miksch Sutton.—Jon C. Barlow, *Editor*

MEMORIAL NOTE

On 21 December 1980, Helen Van Tyne, widow of Josselyn Van Tyne, died in Carmel, California. During her life, most of which was spent in Ann Arbor, Michigan, she was very active in juvenile court matters. Mrs. Van Tyne donated her late husband's extensive library to The Wilson Ornithological Society, where it is now part of the library which bears his name.

AARON M. BAGG STUDENT MEMBERSHIP AWARDS

Student Membership Awards in The Wilson Ornithological Society have been made available through funds generously donated in memory of Aaron M. Bagg, a former president of the society. The Student Membership Committee has designated the award recipients for 1981 as follows: Douglas A. Bell, Westfälische Wilhelms-University, Münster; Thomas Bicak, University of Montana; Scott P. Carroll, University of Oklahoma; Dominick A. Della Sala, Wayne State University; Sylvia L. Halkin, University of Wisconsin; Elizabeth G. Henderson, University of South Carolina; William J. Hilton, Jr., University of Minnesota; Mark L. Hoffman, University of Florida; Charles T. LaRue, Northern Arizona University; David M. Lyons, Frostburg State College, Maryland; Kelvin G. Murray, University of Florida; James S. Quinn, University of Oklahoma; Roland L. Redmond, University of Montana; David E. Seibel, University of Kansas; David A. Spector, Stockton State College, New Jersey; and Kathy A. Winnett-Murray, University of Florida.

FIFTH ANNUAL MEETING OF THE COLONIAL WATERBIRD GROUP

The Colonial Waterbird Group's fifth annual meeting will be held 22–25 October 1981. A symposium on the factors affecting reproductive success in colonial birds is also planned; papers may be submitted to Colonial Waterbirds, the Group's new journal. Symposium abstracts should be sent to J. Burger, Dept. Biology, Livingston College, Rutgers University, New Brunswick, New Jersey 08903 by 1 August 1981; regular session paper abstracts should be received by J. Burger by 1 September 1981. For information on registration, contact Brian Chapman, Dept. Biology, Corpus Christi State University, Corpus Christi, Texas 78412.

SOUTHEASTERN COASTAL AND ESTUARINE BIRDS CONFERENCE-WORKSHOP

This conference-workshop will be held 11–13 September 1981 at the field laboratory of the Belle W. Baruch Institute for Marine Biology and Coastal Research, University of South Carolina, near Georgetown. This meeting will focus on a total ecosystem approach and will assemble past and present federal, state and academic researchers from Delaware, Maryland, Virginia, North and South Carolina, Georgia and Florida in an attempt to determine levels and directions of current research. Results of research on coastal and/or estuarine species, avian prey bases, avian competitors, etc. can be presented in conventional or poster format. Graduate students are especially welcome. A limited number of graduate student awards (room and registration fee waivers) are available. For information on presentations and student awards write Keith Bildstein, Dept. Biology, Winthrop College. Rock Hill, South Carolina 29733 or phone (803) 323–2111. Information on registration and housing will be mailed to A.O.U., W.O.S. and C.O.S. members in the southeast. Others wishing to be placed on the mailing list should write Bobbie Christy, Baruch Field Lab., P.O. Box 1630, Georgetown, South Carolina 29440 or phone (803) 546–3623.

This issue of *The Wilson Bulletin* was published on 14 May 1981.

The Wilson Bulletin

Editor Jon C. Barlow

Department of Ornithology
Royal Ontario Museum
100 Queen's Park
Toronto, Ontario, Canada M5S 2C6

Assistant Editor Margaret L. May

Senior Editorial Assistants Gary Bortolotti
Nancy Flood

Editorial Assistants Keith L. Bildstein
C. Davison Ankney
Richard R. Snell
James D. Rising

Review Editor Robert Raikow
Department of Biological Sciences
University of Pittsburgh
Pittsburgh, PA 15260

Color Plate Editor William A. Lunk
865 North Wagner Road
Ann Arbor, MI 48103

Suggestions to Authors

See Wilson Bulletin, 87:144, 1975 for more detailed "Suggestions to Authors." Manuscripts intended for publication in *The Wilson Bulletin* should be submitted in triplicate, neatly typewritten, double-spaced, with at least 3 cm margins, and on one side only of good quality white paper. Do not submit xerographic copies that are made on slick, heavy paper. Tables should be typed on separate sheets, and should be narrow and deep rather than wide and shallow. Follow the AOU Check-list (Fifth Edition, 1957) and the 32nd Supplement (Auk, 90:411–419, 1973), insofar as scientific names of U.S. and Canadian birds are concerned. Summaries of major papers should be brief but quotable. Where fewer than 5 papers are cited, the citations may be included in the text. All citations in "General Notes" should be included in the text. Follow carefully the style used in this issue in listing the literature cited; otherwise, follow the "CBE Style Manual" (1972, AIBS). Photographs for illustrations should have good contrast and be on gloss paper. Submit prints unmounted and attach to each a brief but adequate legend. Do not write heavily on the backs of photographs. Diagrams and line drawings should be in black ink and their lettering large enough to permit reduction. Original figures or photographs submitted must be smaller than 22 × 28 cm. Alterations in copy after the type has been set must be charged to the author.

Notice of Change of Address

If your address changes, notify the Society immediately. Send your complete new address to Ornithological Societies of North America, % Sandra L. L. Gaunt, Box 21160, Columbus, Ohio 43221.

The permanent mailing address of the Wilson Ornithological Society is: c/o The Museum of Zoology, The University of Michigan, Ann Arbor, Michigan 48109. Persons having business with any of the officers may address them at their various addresses given on the back of the front cover, and all matters pertaining to the Bulletin should be sent directly to the Editor.

Membership Inquiries

Membership inquiries should be sent to Dr. Robert C. Whitmore, Division of Forestry, West Virginia University, Morgantown, West Virginia 26506.

CONTENTS

OBSERVATIONS OF SEABIRDS DURING A CRUISE FROM ROSS ISLAND TO ANVERS ISLAND, ANTARCTICA ---- *Robert M. Zink* 1

DISPLAY BEHAVIOR OF OVENBIRDS (*Seiurus aurocapillus*) II. SONG VARIATION AND SINGING BEHAVIOR ---- *M. Ross Lein* 21

THE MAYFIELD METHOD OF ESTIMATING NESTING SUCCESS: A MODEL, ESTIMATORS AND SIMULATION RESULTS ---- *Gary L. Hensler and James D. Nichols* 42

NARROWLY DISJUNCT ALLOPATRY BETWEEN BLACK-CAPPED AND CAROLINA CHICKADEES IN NORTHERN INDIANA ---- *Peter G. Merritt* 54

TOE FUSION IN OSCINES ---- *George A. Clark, Jr.* 67

ENVIRONMENTAL EFFECTS ON ROOSTING BEHAVIOR OF CHIMNEY SWIFTS *Richard M. Zammuto and Edwin C. Franks* 77

GENERAL NOTES

OBSERVATION OF A BROOD OF SHARP-SHINNED HAWKS IN ONTARIO, WITH COMMENTS ON THE FUNCTIONS OF SEXUAL DIMORPHISM *Helmut C. Mueller, Nancy S. Mueller and Patricia G. Parker* 85

FOOD DEPRIVATION AND TEMPERATURE REGULATION IN NESTLING FERRUGINOUS HAWKS *Diana F. Tomback and Joseph R. Murphy* 92

AERIAL "PLAY" OF BLACK VULTURES ---- *Walter A. Thurber* 97

THE SHOULDER-SPOT DISPLAY IN RUFFED GROUSE ---- *Allan Garbutt* 98

THE AGONISTIC REPERTOIRE OF SANDHILL CRANES *Stephen A. Nesbitt and George W. Archibald* 99

NOTES ON THE SLENDER ANTBIRD ---- *Edwin O. Willis and Yoshika Oniki* 103

NOTES ON THE UNIFORM CRAKE IN COSTA RICA ---- *F. G. Stiles* 107

TRICHOMONIASIS IN BALD EAGLES ---- *Ward B. Stone and Peter E. Nye* 109

Protocalliphora INFESTATION IN BROAD-WINGED HAWKS *Scott Crocoll and James W. Parker* 110

HERRING GULL ATTACKS AND EATS ADULT MALE OLDSQUAW ---- *Richard R. Snell* 110

RED-LEGGED KITTIWAKES FORAGE IN MIXED-SPECIES FLOCKS IN SOUTHEASTERN ALASKA ---- *Douglas Siegel-Caŭsey and Thomas E. Meehan* 111

GROUND-FEEDING METHODS AND NICHE SEPARATION IN THRUSHES ---- *Alan Tye* 112

AMERICAN COOT DISTRIBUTION AND MIGRATION IN COLORADO *Warner P. Gorenzel, Ronald A. Ryder and Clait E. Braun* 115

REPRODUCTIVE RATE AND RENESTING OF RED-WINGED BLACKBIRDS IN MINNESOTA *Daniel W. Moulton* 119

MIGRATION SPEEDS OF THREE WATERFOWL SPECIES *Frank C. Bellrose and Robert C. Crompton* 121

ORNITHOLOGICAL LITERATURE ---- 125

ORNITHOLOGICAL NEWS ---- 135

WIL
8424
.a

MUS. COMP. ZOOL
LIBRARY
SEP 9 1981
HARVARD
UNIVERSITY

The Wilson Bulletin

PUBLISHED BY THE WILSON ORNITHOLOGICAL SOCIETY

VOL. 93, NO. 2 JUNE 1981 PAGES 137–300

THE WILSON ORNITHOLOGICAL SOCIETY

FOUNDED DECEMBER 3, 1888

Named after ALEXANDER WILSON, the first American Ornithologist.

President—George A. Hall, Department of Chemistry, West Virginia University, Morgantown, West Virginia 26506.

First Vice-President—Abbot S. Gaunt, Department of Zoology, Ohio State University, Columbus, Ohio 43210.

Second Vice-President—Jerome A. Jackson, Department of Biological Sciences, P.O. Drawer Z, Mississippi State University, Mississippi State, Mississippi 39762.

Editor—Jon C. Barlow, Department of Ornithology, Royal Ontario Museum, 100 Queen's Park, Toronto, Ontario, Canada M5S 2C6.

Secretary—Curtis S. Adkisson, Department of Biology, Virginia Polytechnic Institute and State University, Blacksburg, Virginia 24061.

Treasurer—Robert D. Burns, Department of Biology, Kenyon College, Gambier, Ohio 43022.

Elected Council Members—Sidney A. Gauthreaux, Jr. (term expires 1981); Richard C. Banks (term expires 1982); Mary H. Clench (term expires 1983).

Membership dues per calendar year are: Active, $16.00; Student, $14.00; Sustaining, $25.00; Life memberships $250 (payable in four installments).

THE WILSON BULLETIN is sent to all members not in arrears for dues.

THE JOSSELYN VAN TYNE MEMORIAL LIBRARY

The Josselyn Van Tyne Memorial Library of the Wilson Ornithological Society, housed in the University of Michigan Museum of Zoology, was established in concurrence with the University of Michigan in 1930. Until 1947 the Library was maintained entirely by gifts and bequests of books, reprints, and ornithological magazines from members and friends of the Society. Now two members have generously established a fund for the purchase of new books; members and friends are invited to maintain the fund by regular contribution, thus making available to all Society members the more important new books on ornithology and related subjects. The fund will be administered by the Library Committee, which will be happy to receive suggestions on the choice of new books to be added to the Library. William A. Lunk, University Museums, University of Michigan, is Chairman of the Committee. The Library currently receives 195 periodicals as gifts and in exchange for *The Wilson Bulletin*. With the usual exception of rare books, any item in the Library may be borrowed by members of the Society and will be sent prepaid (by the University of Michigan) to any address in the United States, its possessions, or Canada. Return postage is paid by the borrower. Inquiries and requests by borrowers, as well as gifts of books, pamphlets, reprints, and magazines, should be addressed to: The Josselyn Van Tyne Memorial Library, University of Michigan Museum of Zoology, Ann Arbor, Michigan 48109. Contributions to the New Book Fund should be sent to the Treasurer (small sums in stamps are acceptable). A complete index of the Library's holdings was printed in the September 1952 issue of *The Wilson Bulletin* and newly acquired books are listed periodically. A list of currently received periodicals was published in the December 1978 issue.

THE WILSON BULLETIN
(ISSN 0043-5643)

The official organ of the Wilson Ornithological Society, published quarterly, in March, June, September, and December. The subscription price, both in the United States and esewhere, is $20.00 per year. Single copies, $4.00. Subscriptions, changes of address and claims for undelivered copies should be sent to the Treasurer. Most back issues of the *Bulletin* are available and may be ordered from the Treasurer. Special prices will be quoted for quantity orders.

All articles and communications for publications, books and publications for reviews should be addressed to the Editor. Exchanges should be addressed to The Joselyn Van Tyne Memorial Library, Museum of Zoology, Ann Arbor, Michigan 48109. Known office of publication: Department of Zoology, Ohio State University, 1827 Neil Avenue, Columbus, Ohio 43210.

Second class postage paid at Columbus, Ohio and at additional mailing office.

© Copyright 1981 by the Wilson Ornithological Society

Printed by Allen Press, Inc., Lawrence, Kansas 66044, U.S.A.

The Rufous-faced Crake *(Laterallus xenopterus)* and its Paraguayan congeners, the Red-and-White Crake *(L. leucopyrrhus)* top, the Gray-breasted Crake *(L. exilis)* middle left, and the Rufous-sided Crake *(L. melanophaius)* middle right. The Rufous-faced Crake is shown two-thirds life size and the last three, one-third life size. From a painting by William A. Lunk.

THE WILSON BULLETIN
A QUARTERLY MAGAZINE OF ORNITHOLOGY
Published by the Wilson Ornithological Society

VOL. 93, NO. 2 JUNE 1981 PAGES 137–300

Wilson Bull., 93(2), 1981, pp. 137–144

THE RUFOUS-FACED CRAKE (*LATERALLUS XENOPTERUS*) AND ITS PARAGUAYAN CONGENERS

ROBERT W. STORER

The Black Rail (*Laterallus jamaicensis*) and other crakes of the genus *Laterallus* are among the least known American birds, and Ripley (1977:192) points out that "of all the rail family, this group of species collectively is the least studied." This is not surprising because they are secretive birds living in dense grassy places. But one relatively tame species, the Galapagos Rail (*L. spilonotus*) has been well studied in the field (Franklin et al. 1979). A second species, the Red-and-White Crake (*L. leucopyrrhus*) is commonly kept in aviaries where some of its habits have been reported (Meise 1934, Everitt 1962, Levi 1966). Museum specimens of *Laterallus* are few, hence their distribution and status are poorly known; anatomical material is even scarcer.

The least known species of the group, the Rufous-faced Crake (*L. xenopterus*), was first taken in Paraguay in 1933 and described the following year (Conover 1934). It was not found again until Philip Myers rediscovered it in 1976 and Rick Hansen in 1978 (Myers and Hansen 1980). The species has not been illustrated previously, probably because the tail was missing from the type specimen and information on the color of the soft parts was not available.

In 1979, I spent 5 weeks in Paraguay with a field party from the University of Michigan Museum of Zoology led by Philip Myers, III. One of my aims was to collect and find out as much as possible about the secretive crakes of this country. Two other species of *Laterallus*, the Red-and-White Crake and the Rufous-sided Crake (*L. melanophaius*), were already known from Paraguay. On my last day in the field, Dr. Myers presented me with a fresh specimen of the Gray-breasted Crake (*L. exilis*). The nearest localities from which this bird was previously known are in the

Amazon Valley, nearly 1500 miles to the north. Although we never heard or saw a crake in the wild, we captured specimens of all four in mammal traps and were able to obtain information on habitat, associated mammals and soft-part colors (the last by photographing fresh specimens in color). Study skins and these photographs were used by William A. Lunk in preparing the accompanying plate. Specimens of all the known species of *Laterallus* were examined in or borrowed from the following museums: American Museum of Natural History (AMNH), Field Museum of Natural History, Museum of Comparative Zoology, Academy of Natural Sciences of Philadelphia and National Museum of Natural History.

The colors and patterns of the 4 Paraguayan species are well shown in the plate. Of particular interest are those of the under tail coverts, which are black in *L. xenopterus*, black barred with white in *L. exilis*, rufous in *L. melanophaius*, and white laterally and black medially in *L. leucopyrrhus*. These feathers are displayed conspicuously during tail bobbing, a common behavior pattern in rails, which is known for at least *L. leucopyrrhus* (Levi 1966:25) and *L. spilonotus* (Franklin et al. 1979:213–214). Presumably it occurs in all species, and it may be important in species recognition.

The heavy, white barring on the scapulars and upper wing coverts is one of the striking characteristics of the Rufous-faced Crake and is presumably the basis for the specific name *xenopterus* (xen- = strange, pteron = wing). Although I can find no reference in the literature to barring on the upper surface of the wings of the other Paraguayan species of *Laterallus*, barring is found in varying degrees on at least a few examples of each. The Red-and-White Crake is the most variable in this barring. The wing coverts of 1 specimen (AMNH 472,173) are extensively and irregularly marked with white bars up to 4 mm in width that are bordered with narrower black bars. Two other examples have white bars 2–2.5 mm wide, 5 have bars less than 2 mm wide and 6 lack white bars. In addition, 13 of 20 specimens of *L. leucopyrrhus* have diffuse rufous barring on the wing coverts. Rufous-sided Crakes also may have narrow barring on the upper wing coverts and scapulars: 9 specimens I examined have well-marked barring, 16 have faint barring and 32 are unbarred. In all instances the barring was narrow, the white bars being less than 2 mm in width. Gray-breasted Crakes show a variable amount of narrow white barring on the upper wing coverts. Specimens used in preparing the plate included those showing the maximum amount of white barring found in *L. melanophaius* and *L. exilis*. This was done to emphasize the occurrence of this patterning.

Measurements of the 4 Paraguayan forms of *Laterallus* are given in Table 1. Although males average slightly larger than females, data for the

TABLE 1

MEASUREMENTS (IN MM) AND WEIGHTS (IN G) OF PARAGUAYAN SPECIES OF *LATERALLUS*

		N	Range	$\bar{x}$	SD
Wing	*exilis*	12	69–78	72.0	±2.73
	melanophaius	40	74–90	82.9	±3.30
	leucopyrrhus	18	80–86	82.4	±1.82
	xenopterus	4	83–91	86.5	±3.42
Bill from nostril	*exilis*	12	7.7–8.8	8.29	±0.33
	melanophaius	40	9.5–11.5	10.47	±0.62
	leucopyrrhus	18	8.1–9.8	9.03	±0.56
	xenopterus	4	7.5–8.7	8.00	±0.50
Bill depth	*exilis*	9	4.7–5.8	5.17	±0.39
	melanophaius	26	5.2–6.7	5.91	±0.42
	leucopyrrhus	15	5.1–6.6	5.75	±0.34
	xenopterus	4	5.9–6.2	6.03	±0.13
Tarsus length	*exilis*	11	22.5–26.0	24.07	±0.95
	melanophaius	40	28.4–35.3	31.44	±1.59
	leucopyrrhus	18	30.1–35.0	32.82	±1.23
	xenopterus	4	28.3–30.6	29.73	±1.07
Length middle toe	*exilis*	12	24.8–28.4	26.43	±1.09
	melanophaius	39	29.0–38.0	33.63	±1.85
	leucopyrrhus	15	29.6–35.1	31.41	±1.22
	xenopterus	4	27.4–28.9	28.35	±0.69
Weight	*exilis*	3	27–28	27.53	—
	melanophaius	2	46–56.6	51.30	—
	leucopyrrhus	10	34–52	45.35	±5.61
	xenopterus	3	51–53	52.00	—

sexes are combined in the table because of small size of some samples and the high proportion of unsexed specimens of *L. exilis*. Aside from differences in size indicated by wing length and weight, several differences in proportions are evident. *L. melanophaius* is notably long-billed, whereas *L. xenopterus* has a very short, high bill, as well as a relatively short tarsus and middle toe. The last two are probably associated with the species' habitat, which is densely vegetated and has a relatively firm substrate.

HABITAT

The dense, tussock-like habitat of the Rufous-faced Crake has been well described by Myers and Hanson (1980). The Red-and-White Crake was taken in the same habitat near Curuguaty, Dept. Canendiyu, and was also taken in an adjacent wetter part of the marsh among tall (2 m +)

coarse grass with scattered tree ferns. Others were taken near Tobatí, Dept. Cordillera, in a heavily grazed marsh with relatively short (50 cm) grasses over damp ground and in a coarser marsh with dense, tall (2 m+) grasses and some shrubs. All were captured in traps set in runways made through the grass by small mammals or water runoff. We encountered the Rufous-sided Crake only on the Arroyo Hondo, 24 km NNW of Carayao, Dept. Caaguazu. The 2 specimens were taken in traps on the edge of a marsh between open water with scattered vegetation and dense grasses approximately 1 m tall. Erickson and Mumford (1976:8–9) reported taking both Red-and-White and Rufous-sided crakes in the same cattail marsh at Vicosa, Minas Gerais, Brazil. The Gray-breasted Crake was taken in a runway used by swamp rats (*Holochilus brasiliensis*) along a fencerow bordering a road and a heavily grazed marsh with water depths ranging from a few centimeters to several feet. The marsh contained a mixed growth of several kinds of grasses and/or sedges. Miller (1960:235) reported collecting a Gray-breasted Crake "as it fluttered from marsh vegetation 50 cm high where the water was 10 to 15 cm deep."

From the few accounts available, it appears that the habitat of the Rufous-faced Crake may be the most restricted of the four, whereas the Rufous-sided and Red-and-White crakes are found in more varied habitat which often includes sparser vegetation and deeper water.

DISTRIBUTION

The Rufous-sided Crake is the most widely distributed of the Paraguayan species, both within the country and in South America. It is also the best represented in collections. It is found in suitable habitats throughout South America, south at least to central Argentina (near Buenos Aires) and southern Uruguay. In Paraguay, it has been recorded both in the eastern part of the country and the Chaco to the west.

The Red-and-White Crake is known from the vicinity of Rio de Janeiro south to Buenos Aires and west to eastern Paraguay. It has not been recorded from the Chaco. The record from Tucumán is in error (Olrog 1963:125). The bird is locally common and is frequently kept in zoos and aviaries.

The Rufous-faced Crake has the most limited known distribution of the four, having been taken at 3 localities in eastern Paraguay and 1 in Brazil (Myers and Hansen 1980). The locality shown on the map in Ripley (1977:205) is in error. Presumably, it was meant to show the type locality, Horqueta, Paraguay, but the locality is actually shown in Brazil.

The Gray-breasted Crake has been recorded from British Honduras to Paraguay. The single Paraguayan specimen was taken 6 August 1979, in the pantanal (palm swamp region), 24 km NW of Villa Hayes (Dept. Pres-

idente Hayes). Whether it was a migrant, a stray, or part of a resident population is unknown.

GENERIC LIMITS

Of the 10 species included in *Laterallus* by Peters (1934:189–192) one, "*hauxwelli*" (= *fasciatus*) (Black-banded Crake), has been considered a species of *Anurolimnas* by Stresemann and Stresemann (1966:149), who followed the lead of Sharpe (1894:88), and by Olson (1973:393), who felt that *viridis* (Russet-crowned Crake) also was closer to the latter genus than to *Laterallus*. Ripley (1977:157–158, 192–194), without stating his reasons, placed *castaneiceps* (Chestnut-headed Crake), the type species of *Anurolimnas*, in *Rallina* and left *fasciatus* and *viridis* in *Laterallus*. After examining specimens of the species involved, I find Olson's arguments reasonable and prefer to retain *fasciatus* and *viridis* in *Anurolimnas* with *castaneiceps* at least for the present. More recently, Blake (1977:501) has included the species *spilopterus* (Dot-winged Crake) in *Laterallus*. Although this species was described in *Laterallus*, it has long been kept in *Porzana*, on the basis of its plumage color and pattern. I know of no anatomical material of this rarely taken species, and tentatively consider it properly placed in *Porzana*. This leaves 9 species in *Laterallus*: *jamaicensis*, *spilonotus*, *exilis*, *albigularis*, *melanophaius*, *levraudi* (Rusty-flanked Crake), *ruber* (Ruddy Crake), *leucopyrrhus* and *xenopterus* (the last described too late for inclusion in Peters 1934).

SPECIES RELATIONSHIPS

The relationships among the species have never been carefully reviewed. If the species are grouped by the color of the under tail coverts they fall into groups which can be further defined on the basis of other characters. Although differing in proportions, *L. spilonotus* is clearly an insular derivative of *L. jamaicensis* and need not be discussed further. Three species, *L. melanophaius*, *L. levraudi* and *L. ruber*, have unmarked rufous under tail coverts. All three are large (for *Laterallus*) and have relatively long, slender bills. The Venezuelan species *L. levraudi* is almost entirely allopatric with *L. melanophaius* and differs from that species in having rufous, instead of black-and-white barred flanks. This difference parallels that between Paint-billed (*Neocrex erythrops*) and Colombian (*N. colombianus*) crakes, which are considered conspecific by some authors (e.g., Meyer de Schauensee 1970, Short 1975) and full species by others (e.g., Blake 1977, Ripley 1977). If not considered conspecific, they are best thought to form a superspecies. I recommend similar status for *L. levraudi* and *L. melanophaius*. *L. ruber* is more distinct, differing from *L.*

levraudi in having a gray head and completely rufous underparts. It may be a Central American representative of the *melanophaius* group.

L. albigularis, *L. exilis* and *L. jamaicensis* all have black and white barred under tail coverts, are small and thin billed and have rufous nape patches. *L. albigularis* has often been considered conspecific with *L. melanophaius*, which differs from it in color of the under tail coverts, uniformly colored upper parts and larger size. I believe that *L. albigularis* is closest to *L. exilis*, differing primarily in the rufous vs gray breast. *L. jamaicensis* is also close to *L. exilis* and *L. albigularis*, but differs considerably in the spotting and barring of the upper parts.

In addition to its tail-covert pattern, *L. leucopyrrhus* differs from its congeners in having bright coral red legs and in laying unspotted eggs. (The eggs of *L. levraudi* and *L. xenopterus* are unknown.)

L. xenopterus differs from the other species in its blue-gray legs and bill, white-barred wing coverts and scapulars, buffy chest, short, high bill, and short tarsi (as pointed out by Conover 1934). The high, arched culmen is evident in the skeleton, as is the short, more domed cranium. This species is the most divergent member of the genus, but at this stage I see no advantage in removing it from *Laterallus*.

Not only has there been little agreement about which species belong in *Laterallus*, but sequences used by various authors also have differed considerably. In Table 2 are shown 3 earlier sequences plus one which expresses my beliefs concerning the relationships among the species indicated earlier. Of the 3 other arrangements shown, only that of Peters (1934) places *L. exilis* next to *L. albigularis* and none place *L. levraudi* next to *L. melanophaius*. Furthermore, Ripley (1977) separates *L. jamaicensis* from its derivative, *L. spilonotus*, by *L. melanophaius*, *L. albigularis* and *L. leucopyrrhus*, which are not closely related either to each other or to the 2 species they separate.

SUMMARY

Four species of *Laterallus* (*melanophaius*, *leucopyrrhus*, *xenopterus* and *exilis*) are known from Paraguay. *L. melanophaius* is found in both the Chaco and eastern Paraguay, whereas *L. leucopyrrhus* and *L. xenopterus* have only been recorded east of the Rio Paraguay. *L. exilis* is here reported for the first time from the country. *L. xenopterus* differs from the other three in having a relatively short, high bill and short tarsi and toes. The latter may be an adaptation for moving about on a firmer substrate.

The species of the genus can be placed into 4 groups on the basis of the color and pattern of the under tail coverts. Other color characters and similarities of proportions within the groups are further indications of the naturalness of the grouping.

ACKNOWLEDGMENTS

I am particularly grateful to Philip Myers, III, for inviting me to accompany him in the field, for collecting many of the specimens here reported on and for help in many other ways.

Table 2

Sequence in *Laterallus*

Peters (1934)	Blake (1977)	Ripley (1977)	This paper
jamaicensis	*spilopterus*[3]	*faciatus*[1]	[*melanophaius*][4]
spilonotus	*jamaicensis*	*levraudi*	[*levraudi*][4]
exilis	*exilis*	*ruber*	*ruber*
albigularis	*xenopterus*	*viridis*[1]	*albigularis*
melanophaius	*albigularis*	*exilis*	*exilis*
ruber	*melanophaius*	*spilonotus*	[*jamaicensis*][4]
levraudi	*ruber*	*melanophaius*	[*spilonotus*][4]
viridis[1]	*levraudi*	*albigularis*	*leucopyrrhus*
hauxwelli[1,2]	*leucopyrrhus*	*leucopyrrhus*	*xenopterus*
leucopyrrhus	*fasciatus*[1]	*jamaicensis*	
	viridis[1]	*xenopterus*	

[1] Here considered species of *Anurolimnas*.
[2] Synonym of *fasciatus*.
[3] Considered by others a species of *Porzana*.
[4] Bracketed species members of superspecies.

Mr. and Mrs. Philip Myers, Jr. provided a welcome base for our operations in Asuncion, and Ed Borjesson, Carlos Centurion and Antonio Espinosa kindly permitted us to carry out fieldwork on their estancias. G. K. Creighton, F. S. Dobson, and Lora, Philip, IV, and Roger Myers assisted with fieldwork. Steven Goodman, Janet Hinshaw, Philip Myers, III, Robert B. Payne and Robert S. Voss read the manuscript and provided valuable comments. An earlier draft of the systematics sections was sent to the American Ornithologists' Union's Committee on the Classification and Nomenclature of North American Birds and to Storrs L. Olson. The fieldwork was supported in part by Grant DEB 77–04887 to Philip Myers, III.

The accompanying color plate, carefully executed by William A. Lunk, not only is the first illustration of *L. xenopterus*, but also provides accurate rendering of the soft-part colors of all 4 species.

LITERATURE CITED

Blake, E. R. 1977. Manual of Neotropical birds. Vol. 1. Univ. Chicago Press, Chicago, Illinois.

Conover, H. B. 1934. A new species of rail from Paraguay. Auk 51:365–366.

Erickson, H. T. and R. E. Mumford. 1976. Notes on birds of the Vicosa, Brazil region. Dept. Forestry and Nat. Res. Agric. Exper. Stat., Purdue Univ. Bull. 131.

Everitt, C. 1962. Breeding the Red-legged Water-Rail. Avic. Mag. 68:179–181.

Franklin, A. B., D. A. Clark and D. B. Clark. 1979. Ecology and behavior of the Galapagos Rail. Wilson Bull. 91:202–221.

Levi, P. J. 1966. Observations on the Southern White-breasted Crake in captivity (*Laterallus leucopyrrhus*). Avic. Mag. 72:24–26.

Meise, W. 1934. Zur Brutbiologie der Ralle *Laterallus leucopyrrhus* (Vieill.) J. Orn. 82:257–268.

Meyer de Schauensee, R. 1970. A guide to the birds of South America. Livingston, Wynnewood, Pennsylvania.

Miller, A. H. 1960. Additional data on the distribution of some Colombian birds. Novedades Colombianas 1:235–237.

Myers, P., III and R. L. Hansen. 1980. Rediscovery of the Rufous-faced Crake (*Laterallus xenopterus*). Auk 97:901–902.

Olrog, C. C. 1963. Lista y Distribucion de las Aves Argentinas. Opera Lilloana 9:1–377.

Olson, S. L. 1973. A classification of the Rallidae. Wilson Bull. 85:381–416.

Peters, J. L. 1934. Check-list of birds of the world. Vol. II. Harvard Univ. Press, Cambridge, Massachusetts.

Ripley, S. D. 1977. Rails of the world. David R. Godine, Boston, Massachusetts.

Sharpe, R. B. 1894. Catalogue of the Fulicariae and Alectorides in the collection of the British Museum. Longmans, London, England.

Short, L. L. 1975. A zoogeographic analysis of the South American chaco avifauna. Bull. Am. Mus. Nat. Hist. 154:165–352.

Stresemann, E. and V. Stresemann. 1966. Die Mauser der Vögel. J. Orn. Sonderheft 107:1–448.

museum of zoology, univ. michigan, ann arbor, michigan 48109. accepted 20 mar. 1981.

COLOR PLATE

The color plate Frontispiece of *Laterallus* spp. by William Lunk has been made possible by an endowment established by George Miksch Sutton.

Wilson Bull., 93(2), 1981, pp. 145–163

RESOURCE USE STRATEGIES OF WADING BIRDS

James A. Kushlan

Ciconiiform wading birds possess several characteristics that make them useful as subjects for ecological studies. They are relatively large birds, ranging from the Least Bittern (*Ixobrychus exilis*), 28 cm long, to the Goliath Heron (*Ardea goliatha*), 140 cm long, (Hancock and Elliott 1978). They are widespread, with some superspecies ranging from the temperate zone through the tropics. They represent a diversity of variations on a general avian theme, that of a long-legged aquatic predator. Their relatively high energy demands and locally large populations make them important components of aquatic ecosystems. Interspecific differences in size, habitat use, sociality, distribution, responses to seasonal environmental pressures and food habits provide the fabric for natural experiments in the elaboration of resource use strategies in aquatic environments.

In this paper, I present a selective review of the current state of knowledge of resource use strategies in wading birds. This report and its companion paper, a review of foraging ecology (Kushlan 1978a), have as their common goal the stimulation of further use of this group of birds for ecological study.

PHYSICAL FACTORS

Short-term weather conditions, such as extreme temperature or rainfall, often constrain resource use in birds (Anderson 1965, Robins 1970). Most adult wading birds appear to be relatively immune to the direct stresses of excessively hot or cold conditions, compared with smaller birds, by virtue of behavioral and physiological adaptations (Kahl 1963, Hafez 1964, Steen and Steen 1965), not the least of which is their relatively large body mass (Calder 1975). Rainfall and cool temperatures may have indirect effects such as delay or interruption of feeding schedules. Consistently cold weather may have the long-term energetic cost of reducing availability of the poikilothermic prey that are commonly consumed by wading birds (Kushlan 1978a), by lessening the prey's activity level, or by driving them into deeper water. Rainfall increases turbidity in waters used by visually foraging birds, which can influence habitat choice and feeding rates (Krebs 1974, Custer and Osborn 1978a, Thompson 1978) and may affect nestling mortality (Owen 1960).

Seasonality, particularly seasonal variation in resource availability, is a dominating feature in the evolution of many species and communities (Beals 1970, Fogden 1972, Leck 1972). The importance of seasonal vari-

ation in weather conditions on wading birds has been conclusively demonstrated for the temperate Grey Heron (*Ardea cinerea*). Mortality, particularly of first-year birds, and resulting population trends of this heron are determined in part by the severity of winter conditions (Lack 1966, Stafford 1971, Reynolds 1979, North 1979).

Seasonal rainfall patterns affect prey availability by causing water levels to fluctuate in shallow-water habitats. Relationships between water level changes and wading bird foraging have been demonstrated for a number of species (Kushlan 1978a). However, most information available is for the Wood Stork (*Mycteria americana*). Kahl (1964) found in the Big Cypress Swamp of Florida that Wood Storks began to nest at a specific water level. Kushlan et al. (1975) found a mathematical relationship between the timing of Wood Stork nesting and the rate of water level decline in the Florida Everglades. A similar relationship was later confirmed in a separate system in central Florida (Clark 1978). The existence of such precise relationship between seasonal hydrologic conditions and nesting phenology of the Wood Stork suggests that seasonal fluctuations in the physical environment may also play a crucial role in the availability of resources to other species of wading birds.

GEOGRAPHY

Geography affects resource use, especially as it influences population size and diversity along latitudinal or continent-to-ocean gradients. For example, the richness of the wading bird guild increases with decreasing latitude in eastern North America (Fig. 1). The data figured are for coastal regions but, as wading birds are primarily coastal in distribution over much of the area, this constraint does not much affect regional species richness. Richness declines rapidly north of 40° N, probably because of adverse climate for wading birds and a decrease in the amount of coastal marshes along the east coast. It has been clearly demonstrated that the amount of habitat available is correlated with both population size (Custer and Osborn 1977, Kushlan 1978a) and colony site location (Lack 1954, Kushlan 1976a, Fasola and Barbieri 1978). Changes in wading bird species richness affect interactions among foraging wading birds, particularly among species that feed aggregately, because the diversity of foraging aggregations increases from temperate to tropical latitudes (Kushlan 1978a).

The drop in species richness between 20 and 25° N in eastern North America (Fig.1) is an exception to the general temperate to tropical pattern. This particular drop occurs on the Florida Keys, an island chain off the lower Florida coast. Such oceanic environments appear to have a lower resource base actually available to a bird that feeds by wading than do extensive, shallow inland or coastal marshes (Kushlan and Robertson

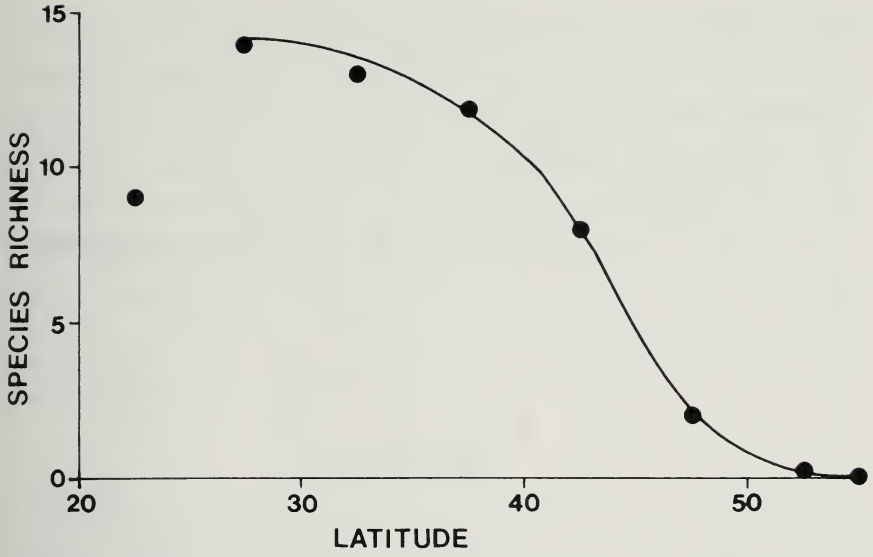


FIG. 1. The relationship between latitude and wading bird species richness in eastern North America. Data analyzed in 5° blocks. Data on nesting species from Custer and Osborn (1977), supplemented for high latitudes by Palmer (1962) and at low latitudes by Green (1946) and Kushlan and Robertson (1977). Isolated point corresponds to the Florida Keys, an oceanic environment.

1977). Recher and Recher (1972) have shown that only a single wading bird, the Reef Heron (*Egretta sacra*), can exist on the Great Barrier Reef, an area of low resource availability to herons, despite its high productivity overall.

POPULATION MOVEMENTS

Movements of individuals and entire segments of populations are tactics commonly employed by wading birds in response to fluctuations in resource availability. Wading birds use up to 3 types of population shifts: migration, dispersal and intraregional movement (Fig. 2).

Seasonal migrations, which may be intercontinental in extent, are well known among wading birds, including such diverse species as the White Stork (*Ciconia ciconia*), White-faced Ibis (*Plegadis chihi*), Green Heron (*Butorides virescens*), Cattle Egret (*Bubulcus ibis*) and other temperate herons (Meyerriecks 1960; Ryder 1967, 1978; Kahl 1972; McClure 1974; Siegfried 1978).

Dispersal of juveniles and adults occurs at the end of nesting. Such dispersal probably results in movement of birds from areas where re-

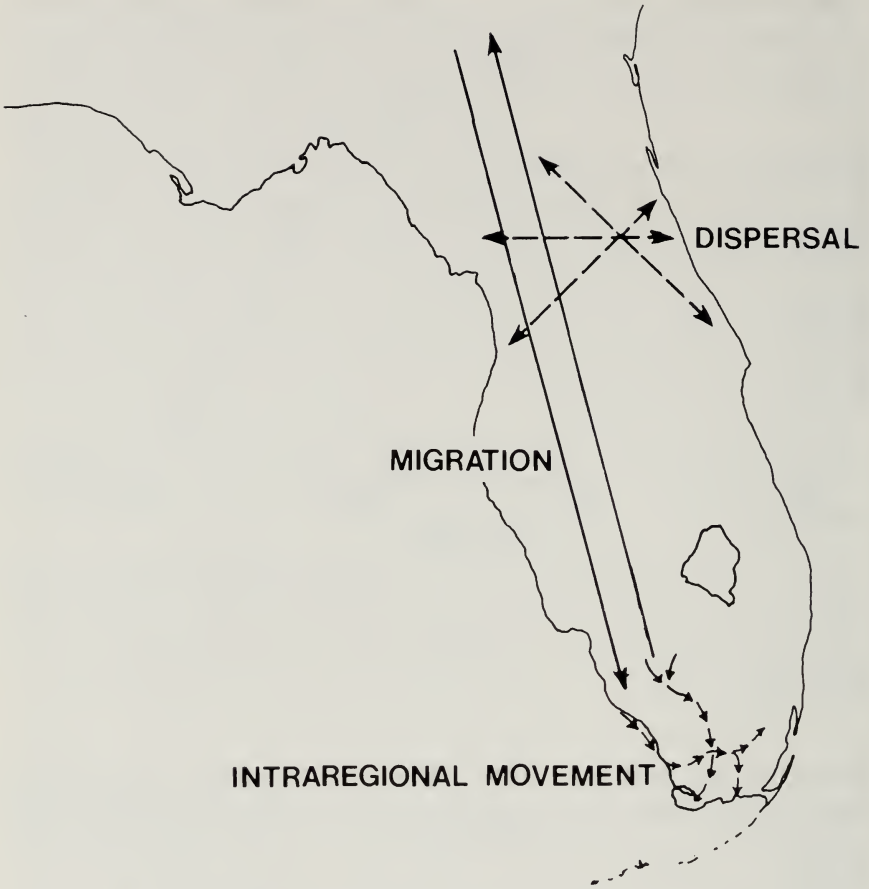


FIG. 2. Movement tactics of wading birds as illustrated by the situation in Florida.

sources are scarce or unavailable to more favorable areas (Byrd 1978). For example, after completing nesting in Florida, birds tend to disperse northward into temperate marshes (Kushlan and Robertson 1977), where food may be approaching its seasonal maximum. As a result, the annual resource base available to the population is increased.

Intraregional movement is a less appreciated component of wading bird foraging tactics (Kushlan 1978a). Such movements have been well documented for species such as the Cattle Egret in Africa, Sacred Ibis (*Threskiornis aethiopica*) in Africa and Australia, Strawnecked Ibis (*T. spinicollis*) in Australia, and White Ibis (*Eudocimus albus*) and Wood Stork in Florida (Carrick 1962, Craufurd 1966, Urban 1974, Ogden et al. 1978, Clark and Clark 1979, Kushlan 1979a).

The relation of the 3 types of population movements to environmental conditions can be illustrated by the pattern shown by the Wood Stork in southern Florida (Kushlan et al. 1975, Ogden et al. 1978). After nesting is completed in spring and early summer, Wood Storks migrate northward, spending the summer and early autumn in north Florida and other coastal plain areas. Return migration takes place later in the fall. On their return to south Florida, storks forage initially in coastal marshes and then begin intraregional movements, moving through a succession of coastal and inland foraging sites throughout the nesting period. These movements correspond with the timing of seasonal drying of various marshes and resulting concentration of fish on which the storks depend (Ogden et al. 1976). Should water levels rise instead of fall, storks abandon their feeding pattern and disperse to scattered sites.

PREDATION

Avoidance of or alertness for potential predators may consume time and energy and may affect the types of foraging activity in which a bird can engage. Healthy adult wading birds are preyed upon rarely and, concomitantly, specific antipredator adaptations appear to be poorly developed (Milstein et al. 1970). For adult wading birds, passive awareness of possible predators generally suffices, supplemented by simple responses such as alert posture, freezing, bill thrusts, bittern stance, ducking and flight. Characteristics such as cryptic coloration, which may serve antipredator functions in other groups, appear most readily explainable as foraging adaptations in wading birds (Kushlan 1978a). Social foraging, common among wading birds, may confer an extra measure of group vigilance through feeding vocalizations that can communicate that "all is well" (Kushlan 1976b). Available reports of successful predation on adult wading birds are often circumstantial (Bent 1937, Monson 1951, Cottrille and Cottrille 1958, Blaker 1969, Milstein et al. 1970, Callahan and Carey 1979). Bayer (1979) presented the best account of a predator, a Bald Eagle (*Haliaeetus leucocephalus*), attacking wading birds, Great Blue Herons (*Ardea herodias*). Although unsuccessful, the eagle's attack and its presence altered the foraging behavior of the herons, leading to the formation of temporary groupings. It appears that the threat of predation is usually not a major determinant of foraging patterns in most wading birds, but this is an aspect of wading bird foraging about which much more information is needed.

Predation threat to nestlings has critical effects on resource use tactics of the parents. A number of predators eat wading bird eggs and nestlings (Baker 1940, Owen 1960, Teal 1965, Dusi and Dusi 1968, Dickerman and Gavino 1969, Blaker 1969, Milstein et al. 1970, Taylor and Michael 1971).

Black-crowned Night Herons (*Nycticorax nycticorax*) may prey on other species of wading birds nesting in the same colony (Beckett 1964, Teal 1965, Kale 1965, Blaker 1969, Wolford and Boag 1971). Sibling cannibalism also occurs (Dusi 1968). Because of the long growth period and exposed nesting sites, adult wading birds guard chicks past the post-hatching brooding period (Milstein et al. 1970). The need for such nest attendance affects resource use in 2 major ways. During the guarding period, growth rates are relatively rapid until biomass growth and organ development are such as to permit the chicks to be left alone (Kushlan 1977a, b; Werschkul 1979). Adult nest-guarding also requires that the burden of early food gathering fall to the non-guarding adult, which in Wood Storks may also feed the attending parent (Kahl 1966). The female White Ibis tends to forage during the middle of the day while the larger male guards the nest (Kushlan 1976c, 1977c). If such a schedule imposes time and energy constraints on the adults, the need for effective foraging may become increasingly critical during this period of nesting. When young achieve the size and locomotor maturity that permits independence of parental guardianship, both parents can forage at the same time, which should increase the amount of food available to young (Owen 1955, Siegfried 1972, Kushlan 1977b) or decrease stress on adults (Werschkul 1979).

FORAGING SOCIALITY

Wading birds forage alone or in groups of varying size. Large aggregations of wading birds form at sites of high prey availability (Kushlan 1976a). By foraging in an aggregation, wading birds probably decrease search time between food patches, increase the likelihood of foraging in a suitable location, decrease risk of obtaining no food and perhaps have more potential food available (Kushlan 1978a). Some species have characteristics, such as white plumage, that aid in establishing aggregations by attracting other birds to feeding sites (Kushlan 1977d).

Aggregated foraging permits efficient use of the ephemeral resources that characterize many wading bird habitats. The amount and distribution of resources and their availability change markedly on a daily or seasonal basis such that wading birds may be able to feed on these resources for only relatively short periods at a time. By aggregating, birds find and use these locations as they become available. In south Florida, seasonal changes in prey availability cause aggregations to form daily at newly suitable sites and, as a result, the birds sequentially use much of the habitat available over the annual drying cycle (Kushlan 1976b, 1979a).

Aggregative foraging also brings birds into close proximity and increases social interactions (Grubb 1976, Woolfenden et al. 1976, Kushlan 1978b, Russell 1978). Wading birds reserve a feeding space within an aggregation

by continuing to defend individual distances. The amount or types of resources consumed within aggregations could increase, decrease, or be unchanged depending on the circumstances. I have proposed (Kushlan 1978a) that within an aggregation some wading birds gain a net energy benefit with increasing aggregation size up to some maximum. Such an increase may possibly be due to a subtle commensal benefit derived from nearby birds, similar to that noted below. The point of maximum commensal benefit may be determined by increasing interference among the birds. The influence of the 2 effects depends on the number of birds present, feeding tactics employed by each species and prey availability. An increased return from aggregative foraging has been demonstrated for Little Blue Herons (*Florida caerulea*) foraging with White Ibis (Kushlan 1978b) and for Snowy Egrets (*Leucophoyx thula*) and Great Egrets (*E. alba*) foraging with Roseate Spoonbills (*Ajaia ajaja*) (Russell 1978). Many other possibly commensal associations have been reported in wading birds (Kushlan 1978a). Krebs (1974) studied the intake of Great Blue Herons feeding within and outside of aggregations in an attempt to determine whether aggregating was beneficial. Unfortunately, his results were equivocal. DesGranges (1978) found higher feeding rates when Great Blue Herons fed in larger than in smaller groups. This result supports the possibility that there may be a commensal advantage to feeding in aggregations. Interference phenomena have been documented by Goss-Custard (1970) for shorebirds, but their occurrence in wading birds requires study. Russell (1978) suggested that the subordinate position of Snowy Egrets in mixed aggregations reduced their potential increase in net energy gain. Similarly, piracy, such as Great Egret piracy on White Ibis (Kushlan 1978c), adversely affects foraging efficiency and presumably energy gain of the victim.

The relationship between aggregation size and energy gain should differ among wading bird species. A species with a foraging repertoire composed of behaviors that are effective within aggregations could increase its energy intake with increasing aggregation size. Other species, such as standing-feeders or active-feeders whose behavior brings them into conflict with larger standing-feeding birds, would have the effectiveness of their foraging decreased as aggregation size increases. Such species may, however, "parasitize" aggregations of other birds by using them to find patches of abundant prey and then feeding near, but not within the aggregation (Kushlan 1977d).

COMPETITION

The role of indirect competition in channelling resource use patterns in wading birds is unclear. Considering an entire regional wading bird com-

munity, species can be shown to partition resources through a combination of characteristics, including habitat, time of feeding, general feeding strategy (visual or tactile), size of bird and feeding behavior (Kushlan 1978a). Studies of more compact species groups, such as sympatric herons or ibis, have shown that species differ by size, food, feeding location, or behavior (Carrick 1959, Meyerriecks 1962, Jenni 1969, Kahl 1972, Kushlan 1976b, Willard 1977, Custer and Osborn 1978a, Thompson 1978, Hoffman 1978). However, it remains useful to consider the degree of overlap among sympatric species. Resources generally appear to be divided with a low degree of overlap among herons of different sizes (Willard 1977) and between ibis and storks using similar feeding behavior (Kushlan 1979b). However, overlap in food and habitat among certain, similarly-sized herons has been found to be high in specific instances (Jenni 1962, Willard 1977, Custer and Osborn 1978a). Such overlap need not imply competition in itself, as little is known about the resource state in these cases, but it does suggest the desirability of additional study to determine whether any competition may be involved.

The effect of direct competition on resource division may be especially critical within a feeding aggregation; there have been no studies that clearly show how resources are actually shared or whether competition occurs in such situations. Kushlan (1976b) showed that 7 species (Great Blue Heron, Great Egret, Snowy Egret, Little Blue Heron, Louisiana Heron [*Hydranassa tricolor*], Wood Stork and White Ibis) differed by location, water depth or behavior while feeding together. These differences suggest, although do not prove, that in this case the birds were taking different segments of the available resource spectrum. Competition certainly does occur at times. In the above example, Black-crowned Night Herons, which overlapped in foraging characteristics with Snowy Egrets, did not use the site while the aggregation fed there, probably because of dominance by Great Egrets (Kushlan 1973a). When resources are limited, competition among Cattle Egrets clearly resulted in differential resource allocation to older, more competitively dominant birds (Woolfenden et al. 1976). These results suggest that direct interference competition may be widespread among wading birds.

FORAGING TACTICS

Where to search.—An important consideration in understanding wading bird searching tactics is that habitat and prey for most species are distributed in spatial and temporal patches (Kushlan 1976a). As a result, wading birds need to sample potential patches to decide where to forage. For species such as the White Ibis, choice of foraging patch may in some cases be a primary factor in foraging optimization (Kushlan 1979a). The

energy penalty for wrong choices may be rather severe, because of the relatively high costs incurred by large birds in moving from place to place. Thus, there is probably considerable pressure for wading birds to sample foraging patches efficiently.

Several tactics are employed by wading birds in patch selection. A number of species typically travel and forage in single species flocks. Cattle Egrets (Siegfried 1971, 1978) and White Ibis (Kushlan 1979a) are notable examples. Custer and Osborn (1978b) found that these 2 species often flew in interspecific groups to feeding sites in contrast with 8 other wading bird species. It has been proposed that information regarding the location of food patches is transferred among wading birds at colony and roost sites (Krebs 1974). At least some cirumstantial evidence supports this hypothesis (Krebs 1974, Custer and Osborn 1978b, DesGranges 1978). Information is no doubt transfered in flight lines and at foraging sites as 1 bird sees another feeding. Species that feed in aggregations typically choose sites where other birds are foraging (Kushlan 1977d).

Other tactics used to decrease the frequency of wrong sampling choices include trial and error, learning, return to previously used patches, territoriality and sequential sampling. The dynamics of wading birds foraging in a temporally changing patch demonstrated the role of trial and error (Kushlan 1976a). A few wading birds regularly visited the feeding site for short periods when prey abundance was low. As prey became more abundant, feeding time increased and number of wading birds increased until a large aggregation formed. This succession of events suggests that birds were sampling by trial and error. Length of stay in a patch may have been determined by how much food a bird was able to obtain. Similarly, habitat use in the White Ibis appears to be determined in part by the energy value of the food located there (Kushlan 1979a).

Learning probably plays an important role in feeding site selection. The importance of learning to forage effectively is demonstrated by atypical foraging sites being chosen by juveniles (Kushlan and Kushlan 1975) and also by the lowered foraging effectiveness of young birds (Recher and Recher 1969a, Cook 1978a).

Wading birds return to a previously used patch provided its profitability continues to be sufficient (Owen 1955, Bateman 1970, Kushlan 1976b, Cook 1978b). This means that a given patch will be used for a period of time determined by the rates of resource depression and renewal. Prey availability in some patches, such as reef crests used by the Reef Heron (Recher and Recher 1972), may be renewed daily. Daily renewal in some cases permits the development of permanent territory holding systems. A single species of wading bird can use several tactics in its use of foraging patches. Great Blue Herons, for example, in different situations can hold

permanent territories (Bayer 1978), switch between intertidal and terrestrial foraging (Krebs 1974), or show temporal variability in feeding sites used around a colony (DesGranges 1978).

When resource status changes gradually, patches may be sampled sequentially as they become available. As south Florida swamps dry seasonally, birds can use 1 patch until it is depleted and then move to a nearby patch where prey become available later. Intraregional movements exhibited by many wading birds, discussed previously, result from repeated shifts in foraging sites.

The search.—The effectiveness of a wading bird's search for prey is determined in part by the foraging behaviors used. These behaviors, which I have cataloged elsewhere (Kushlan 1978a), can be expected to be chosen to increase net energy gain. Snowy Egrets, for example, apparently select feeding behavior in relation to prey availability (Kushlan 1972). When dissolved oxygen is low, such as in the early morning, fish may have to come to the surface where diffusion provides a higher oxygen concentration (Kushlan 1974). Under these conditions Snowy Egrets feed by standing, a behavior of relatively low cost. However, as oxygen levels increase during the day and fish become less available at the surface, the egrets may have to resort to more energy intensive behavior, such as foot-dragging. Thus, when resources were easily obtained, egrets used an energetically efficient behavior. Use of passive, low cost behaviors for abundant, conspicuous and easily captured prey or use of active, more variable behaviors when prey are less available may be characteristic of wading birds. In one such case, when standing-feeding was the least successful behavior for Snowy Egrets, success was about inversely related to energy expenditure (Kushlan 1973b). If energy gain is proportional to success, then the net energy gain may be about equivalent for each behavior. Birds using various behaviors may all forage effectively, perhaps because individuals may specialize in different behaviors (Kushlan 1973b).

Prey location, selection and pursuit.—The location, pursuit and selection of prey have been the subject of considerable discussion. MacArthur (1972) suggested that if a bird chooses the diet that minimizes average pursuit and search time per gram of prey, a species should be more specialized in a productive environment than in an unproductive one. In support of this hypothesis, MacArthur (1972) used Recher's (unpubl.) data on the Great Blue Heron, which showed that birds took a narrower food size range in a more productive tropical habitat (south Florida), than in a less productive temperate habitat (New York). However, in using this example MacArthur overlooked 2 confounding factors, that the birds of the 2 populations are not the same size and that the ranges of prey available to the 2 populations may not be similar. The Great Blue Heron population resi-

dent in Florida consists of larger birds than in New York. Because they can handle larger prey the larger birds may be expected to take a wider size range of prey in Florida, rather than the smaller range predicted by the productivity hypothesis. Also, the types and sizes of prey available undoubtedly differ between a subtropical marine site and a temperate freshwater site. Should a more limited range of prey exist in 1 site, irrespective of total productivity, the heron should not be expected to take a wider range of prey there.

There are, however, other examples from wading bird studies that may be useful in assessing the relationship of productivity to food selection. When food is most available diet breadth should be restricted (MacArthur 1972). Thus prey taken in a single location in summer, when availability would be high, should be less diverse than in winter when productivity presumably declines. However, Willard's (1977) data on Great Egrets, Great Blue Herons and Snowy Egrets suggest that, during the spring-summer period of higher food availability, prey sizes were more diverse than in fall-winter. Similarly, a greater diversity of prey was taken by White Ibis in presumably more productive coastal habitats than in inland habitats (Kushlan 1979b). These results are not in accord with predictions and are particularly puzzling for searching predators such as Great Egrets and Great Blue Herons, because these birds would minimize search time by taking additional prey when food is scarce. Such apparent discrepancies from predicted results merit further study.

Smaller species should have a more restricted diet because of shorter search times for smaller more abundant prey, while a larger forager should have a longer search time and eat a wider range of prey (MacArthur 1972). In support of this, it appears that large herons do tend to take a wider size range of prey than small herons (Willard 1977).

A species that searches for its prey should be a generalist, whereas a species that pursues its prey should be a specialist (MacArthur 1972). Jenni (1969) showed that for 2 herons of similar size in north Florida the Snowy Egret, the pursuer, was relatively more specialized than the Little Blue Heron, the searcher. Thus, in the same foraging area, the searcher had a more diverse diet, probably because taking each prey encountered decreased search time between prey items. However, the distinction between searcher and pursuer is often not easy to make, because most species can use either tactic at different times or in different habitats.

Pursuit time has been reduced to zero for those wading birds that forage by tactile detection of prey, a strategy that apparently has evolved at least twice in ciconiiform wading birds (Kushlan 1978a, 1979b). The American White Ibis and the Wood Stork are examples of such species (Kahl and Peacock 1963, Kushlan 1977e). Pursuit is nonexistent because the first

contact with prey is the moment of capture. This, of course, makes the decision of where to search and how to search critical to such foragers.

Other species appear to specialize in pursuit strategies. These active foragers, including the Reddish Egret (*Dichromanassa rufescens*), Louisiana Heron and Snowy Egret (Kushlan 1978a), are species that typically run down prey, especially schools of fish. The Reddish Egret appears to specialize in pursuing schooling fish in shallow water. There has been no test of the relative efficiencies of various types of tactics used by wading birds specializing in active pursuit.

MacArthur and Pianka (1966) predicted that a predator should rank prey types according to their energy value per handling time. For the White Ibis in south Florida, handling time for most prey actually consumed is small and, in general, energy content appears to have minimal relevance to prey selection (Kushlan 1979a). This is because, as a tactile forager, the ibis should accept any prey it catches and can consume quickly. Thus, ibis should encounter their environment in a fine-grained way; and, since prey density should control search time in this completely searching predator, ibis should take prey in proportion to the prey's density. However, density is also, in many cases, irrelevant to the ibis, which selectively consume certain species of prey even at very low density (Kushlan 1979a). Prey selection is made in large part on the basis of a potential prey's catchability, that is, the ability of ibis to effect its capture (Kushlan 1979b). Visually foraging wading birds, on the other hand, at least have the potential to rank prey before capturing. However, there is currently little evidence that they do so.

Capture and handling.—The motor patterns associated with capturing, handling and swallowing prey have been summarized elsewhere (Kushlan 1978a). The maximum possible size of prey for a wading bird is not easily determined, since, given sufficient time and freedom from robbing, a wading bird can eat even very large prey, piece-by-piece. Recher and Recher (1969b) suggested that a heron is capable of seizing and holding a fish at least 25% longer than its bill. Smaller birds take more time to handle prey per gram of prey than do larger birds (Kushlan 1978a). Thus, ease of handling may be an important factor in the wider prey size taken by large wading birds.

Schoener (1971) predicted that handling time would be constant below a certain prey size, but for larger prey it becomes an exponential function of prey size. This appears to be so for the White Ibis (Kushlan 1979a). Handling time increases drastically with increasing prey size to the point where the predator becomes satiated or where it becomes uneconomical to eat the prey because of other considerations. In the White Ibis, capturing of large prey by individual birds increases the probability of an

attack by robbers, particularly Great Egrets. This robbing could restrict the diet of the victim, since some typical prey items are lost through robbing and handling time is increased by avoiding the pursuit of the potential robbers. The White Ibis, when feeding in an aggregation, will often drop newly caught large prey rather than attempt handling (Kushlan 1979a). Similarly, Great Blue Herons drop struggling fish (Recher and Recher 1969b).

Recher and Recher (1969b) showed that defensive structures and behavior increase handling time, increase the likelihood of prey escape and decrease the average net energy value of a captured prey item. In the prey of wading birds, structures appear more effective in defense than behavior alone. A prey that has a high handling time should not be added to the diet if its value per time exceeds the mean of previous prey taken in the diet. Great Blue Herons, however, at times take prey requiring high handling time. Recher and Recher (1972) showed that the average weight of food gained by Great Blue Herons for each minute spent subduing and swallowing a puffer (Tetradontidae) was considerably less than the average weight of food obtained for each minute of foraging time. It would be advantageous for herons to ignore fish such as puffers. Some individual Great Blue Herons, however, have learned to subdue puffers by piercing them and consume them even though it is apparently relatively inefficient for them to do so.

Foraging maximization.—Wading birds may prove useful in studies of the tactics used by animals to increase food intake or energy gain. Present information on wading bird foraging suggests areas that merit particular attention. For example, components of prey other than energy may restrict a wading bird's ability to maximize energy at any given time. Marabou Stork (*Leptoptilos crumeniferus*) chicks require calcium, which is obtainable from natural prey but not from the normal marabou food, carrion, (Kahl 1966) which probably could be gathered more efficiently.

Feeding may not be performed in a maximally efficient manner in some cases, such as when it interferes with a wading bird optimizing its entire activity pattern. During pair formation wading birds spend long hours in territorial defense (Burger 1978) and thereby may need to shorten their feeding time, perhaps by choosing poor feeding sites near the colony. Similarly, social dominance interactions in flocking or aggregating wading birds (Woolfenden et al. 1976, Grubb 1976) may decrease the possibility of using the most efficient foraging behavior or feeding site.

Wading birds usually respond dramatically to short-term availability of easily-obtained prey, such as at fish kills where they can feed with high efficiency (Hoffman 1978, Dombe and McFarlane 1978). However, a long-term strategy of optimizing energy return may require ignoring such short-

term energy bonanzas. Great Blue Herons that hold territories during nesting may not be as likely as nonterritorial birds to take advantage of foraging opportunities at such ephemeral food sources (Bayer 1978).

On a long-term basis, an animal must maintain a positive or neutral energy balance. Thus, a wading bird must obtain sufficient energy to offset its energy expenditure. During nesting and feeding young, high foraging efficiency may be required. On the other hand, non-rigorous foraging may be possible when constraints on time or energy budgets are not great (Kushlan 1978c).

Thus, wading birds appear to demonstrate important factors impinging on energy maximization such as non-energetic foraging requirements, complex activity patterns, long-term considerations and short-term behavioral choices. All can affect approaches to increasing net energy gain and as such can provide considerable insight into resource use strategies.

SUMMARY

Wading birds, because of their large size and diversity, appear to offer some promise for unraveling of certain aspects of foraging ecology and resource use strategies. This paper presents a selective review of the current status of knowledge of resource use strategies in ciconiiform wading birds.

Because of their large size, adult wading birds appear to be relatively immune to direct adverse effects of inclement weather, although indirect effects of weather on prey availability are important. Seasonal variation in resource availability can limit population levels of temperate species and is also a dominating influence in tropical populations, where seasonal fluctuation of surface water conditions determine in large part the nature of resource use. Wading bird species richness increases latitudinally toward the tropics and decreases away from continental areas. Population movements, including seasonal migration, radiative dispersal and intraregional movement, are adaptations to variable resource conditions. Predation pressure on nestlings may influence the evolution of growth patterns and time budgets of nesting adults.

Foraging sociality, especially aggregative feeding, is an important aspect of resource use, and may involve commensalism, competitive interactions and interference. Differently-sized wading birds appear to forage differently, but similarly-sized species may show considerable overlap in foraging parameters. Territoriality and aggregative feeding can decrease search time, or increase or decrease foraging effectiveness. Foraging behavior is diverse and variable, and responds to prey availability. Prey selection of wading birds require study, particularly with respect to factors associated with effectiveness of prey choices.

ACKNOWLEDGMENTS

This report is based on a paper presented at The Wilson Ornithological Society Symposium on Resource Use Strategies in Birds, held at Morgantown, West Virginia. I thank J. Barlow, P. Frohring, J. Rising, S. Rohwer and E. Tramer for discussions or comments on this manuscript.

LITERATURE CITED

Anderson, D.W. 1965. Spring mortality in insectivorous birds. Loon 37:134–135.

Baker, R. H. 1940. Crow depredations on heron nesting colonies. Wilson Bull. 62:124–125.

Bateman, D. L. 1970. Movement-behavior in three species of colonial nesting wading birds: a radio telemetric study. Ph.D. diss. Auburn Univ., Auburn, Alabama.

Bayer, R. D. 1978. Aspects of an Oregon estuarine Great Blue Heron population. Pp. 213–217 *in* Wading birds (A. Sprunt, IV, J. C. Ogden and S. Winckler, eds.). Natl. Audubon Soc., New York, New York.

———. 1979. Bald Eagle-Great Blue Heron interactions. Murrelet 60:32–33.

Beals, E. W. 1970. Birds of a *Euphorbia Acacia* woodland in Ethiopia: habitat and seasonal changes. J. Anim. Ecol. 39:277–297.

Beckett, T. A. 1964. Black-crowned Night Heron feeding behavior. Chat 28:93–94.

Bent, A. C. 1937. Life histories of North American birds of prey. U.S. Natl. Mus. Bull. 170.

Blaker, D. 1969. Behaviour of the Cattle Egret *Ardeola ibis*. Ostrich 40:75–129.

Burger, J. 1978. Competition between Cattle Egrets and native North American herons, egrets and ibis. Condor 80:15–23.

Byrd, M. A. 1978. Dispersal and movements of six North American ciconiiforms. Pp. 161–183 *in* Wading birds (A. Sprunt, IV, J. C. Ogden and S. Winckler, eds.). Natl. Audubon Soc., New York, New York.

Calder, W. A., III. 1975. Consequences of body size for avian energetics. Pp. 86–144 *in* Avian energetics (R. A. Paynter, Jr., ed.). Publ. Nutt. Ornithol. Club 15.

Callahan, R. and W. Carey. 1979. Great Horned Owl suspected of preying upon Snowy Egret. Florida Field Nat. 7:29.

Carrick, R. 1959. The food and feeding habits of the Straw-necked Ibis *Threskiornis spinicollis* (Jameson) and the White Ibis *T. molucca* (Cuvier) in Australia. CSIRO Wildl. Res. 4:69–92.

———. 1962. Breeding movements and conservation of ibises *(Threskiornithidae)* in Australia. CSIRO Wildl. Res. 7:71–88.

Clark, E. S. 1978. Factors affecting the initiation and success of nesting in an east-central Florida Wood Stork colony. Proc. Colonial Waterbird Group 2:178–188.

Clark, R. A. and A. Clark. 1979. Daily and seasonal movements of the Sacred Ibis at Pretoria, Transvaal. Ostrich 50:94–103.

Cook, D. C. 1978a. Foraging behavior and food of Grey Herons *(Ardea cinerea)* on the Ythan Estuary. Bird Study 25:17–22.

———. 1978b. Grey Herons *Ardea cinerea* holding feeding territories on the Ythan Estuary. Bird Study 25:11–16.

Cottrille, W. P. and B. D. Cottrille. 1958. Great Blue Herons: behavior at the nest. Misc. Publ. Mus. Zool. Univ. Michigan 102:1–15.

Craufurd, R. Q. 1966. Notes on the ecology of the Cattle Egret *Ardeola ibis* at Rokupr, Sierra Leone. Ibis 108:411–418.

Custer, T. W. and R. G. Osborn. 1977. Wading birds as biological indicators: 1975 colony survey. U.S. Fish Wildl. Serv. Spec. Scientific Rept. Wildl. No. 206.

——— and ———. 1978a. Feeding site description of three heron species near Beaufort, North Carolina. Pp. 355–360 *in* Wading birds (A. Sprunt, IV, J. C. Ogden and S. Winckler, eds.). Natl. Audubon Soc., New York, New York.

——— and ———. 1978b. Feeding habitat use by colonially-breeding herons, egrets, and ibises in North Carolina. Auk 95:733–743.

DesGranges, J. Y. 1978. Adaptive value of social behaviour in the Great Blue Heron *(Ardea herodias)*. Proc. Colonial Waterbird Group 2:192–201.

Dickerman, R. W. and G. Gavino. 1969. Studies of a nesting colony of Green Herons at San Blas, Nayarit, Mexico. Living Bird 8:95–111.

Dombe, A. H. and R. W. McFarlane. 1978. Feeding ecology of Little Blue Herons at a radionuclear-contaminated reservoir. Pp. 361–364 *in* Wading birds (A. Sprunt, IV, J. C. Ogden and S. Winckler, eds.). Natl. Audubon Soc., New York, New York.

Dusi, J. L. 1968. The competition between Cattle Egrets and Little Blue Herons. Alabama Birdlife 16:4–6.

——— and R. T. Dusi. 1968. Ecological factors contributing to nesting failure in a heron colony . Wilson Bull. 80:458–466.

Fasola, M. and F. Barbieri. 1978. Factors affecting the distribution of heronries in northern Italy. Ibis 120:537–540.

Fogden, M. P. L. 1972. The seasonality and population dynamics of equatorial forest birds in Sarawak. Ibis 114:307–343.

Goss-Custard, J. D. 1970. The responses of Redshanks *Tringa totanus* to spatial variations in their prey density. J. Anim. Ecol. 39:91–113.

Green, E. R. 1946. Birds of the lower Florida Keys. Quart. J. Florida Acad. Sci. 8:198–265.

Grubb, T. C., Jr. 1976. Adaptiveness of foraging in the Cattle Egret. Wilson Bull. 88:145–148.

Hafez, E. S. E. 1964. Behavioral thermoregulation in mammals and birds. Int. J. Biometeorology 7:231–240.

Hancock, J. and H. Elliott. 1978. The herons of the world. London Editions, London, England.

Hartwick, E. B. 1976. Foraging strategy of the Black Oystercatcher *Haematopus bachmani*. Can J. Zool. 54:142–155.

Hoffman, R. D. 1978. The diets of herons and egrets in southwestern Lake Erie. Pp. 365–369 *in* Wading birds (A. Sprunt, IV, J. C. Ogden and S. Winckler, eds.). Natl. Audubon Soc., New York, New York.

Jenni, D. A. 1969. A study of the ecology of four species of herons during the breeding season at Lake Alice, Alachua County, Florida. Ecol. Monogr. 39:245–270.

Kahl, M. P. 1963. Thermoregulation in the Wood Stork, with special reference to the role of the legs. Physiol. Zool. 36:141–151.

———. 1964. Food ecology of the Wood Stork (*Mycteria americana*) in Florida. Ecol. Monogr. 34:97–117.

———. 1966. Comparative ethology of the Ciconiidae. Pt. 1. The Marabou Stork, *Leptoptilos crumeniferus* (Lesson). Behaviour 26:76–106.

———. 1972. Comparative ethology of the Ciconiidae. Pt. 4. "Typical storks" (genera *Ciconia*, *Sphenorhynchus*, *Dissoura*, and *Euxenura*). Z. Tierpsychol. 30:225–252.

——— and L. J. Peacock. 1963. The bill-snap reflex: a feeding mechanism in the American Wood Stork. Nature 199:505–506.

Kale, H. W., II. 1965. Nesting predations by herons in a Georgia heronry. Oriole 30:69–70.

Krebs, J. R. 1974. Colonial nesting and social feeding as strategies for exploiting food resources in the Great Blue Heron *(Ardea herodias)*. Behaviour 51:99–134.

Kushlan, J. A. 1972. Aerial feeding in the Snowy Egret. Wilson Bull. 84:199–200.

———. 1973a. Black-crowned Night Heron diving for prey. Florida Field Nat. 1:27–28.

———. 1973b. Bill vibrating—a prey attracting behavior of the Snowy Egret, *Leucophoyx thula*. Am. Midl. Nat. 89:509–512.

———. 1974. Effects of a natural fish kill on the water quality, plankton, and fish population of a pond in the Big Cypress Swamp, Florida. Trans. Am. Fish. Soc. 103:235–243.

———. 1976a. Site selection for nesting colonies by the American White Ibis *Eudocimus albus* in Florida. Ibis 118:590–593.
———. 1976b. Wading bird predation in a seasonally-fluctuating pond. Auk 93:464–476.
———. 1976c. Feeding rhythm in nestling White Ibis. Wilson Bull. 88:656–658.
———. 1977a. Differential growth of body parts in the White Ibis. Auk 94:164–167.
———. 1977b. Growth energetics of the White Ibis. Condor 79:31–36.
———. 1977c. Sexual dimorphism in the White Ibis. Wilson Bull. 89:92–98.
———. 1977d. The significance of plumage colour in the formation of feeding aggregations of ciconiiforms. Ibis 119:361–364.
———. 1977e. Foraging behavior of the White Ibis. Wilson Bull. 89:342–345.
———. 1978a. Feeding ecology of wading birds. Pp. 249–296 *in* Wading birds (A. Sprunt, IV, J. C. Ogden and S. Winckler, eds.). Natl. Audubon Soc., New York, New York.
———. 1978b. Commensalism in the Little Blue Heron. Auk 95:677–681.
———. 1978c. Nonrigorous foraging by robbing egrets. Ecology 59:649–653.
———. 1979a. Foraging ecology and prey selection in the White Ibis. Condor 81:376–389.
———. 1979b. Prey choice by tactile-foraging wading birds. Proc. Colonial Waterbird Group 3:133–142.
——— AND M. S. KUSHLAN. 1975. Food of the White Ibis in southern Florida. Florida Field Nat. 3:31–38.
——— AND W. B. ROBERTSON, JR. 1977. White Ibis nesting in the lower Florida Keys. Florida Field Nat. 5:41–42.
———, J. C. OGDEN AND A. L. HIGER. 1975. Relation of water level and fish availability to Wood Stork reproduction in the southern Everglades. U.S. Geol. Survey, Open-file Rept., Tallahassee, Florida.
LACK, D. 1954. The stability of the heron population. Br. Birds 47:111–119.
———. 1966. Population studies of birds. Oxford Univ. Press, Oxford, England.
LECK, C. F. 1972. Seasonal changes in feeding pressures of fruit and nector-feeding birds in the neotropics. Condor 74:54–60.
MACARTHUR, R. H. 1972. Geographical ecology. Harper and Row, New York, New York.
——— AND E. PIANKA. 1966. On optimal use of a patchy environment. Am. Nat. 100:603–609.
MCCLURE, H. E. 1974. Migration and survival of the birds of Asia. Bangkok, Thailand, U.S. Army Medical Component, SEATO Medical project.
MEYERRIECKS, A. J. 1960. Comparative breeding behaviour of four species of North American herons. Publ. Nutt. Ornithol. Club 2.
———. 1962. Diversity typifies heron feeding. Nat. Hist. 71(6):48–59.
MILSTEIN, P. LE S., I. PRESTT AND A. A. BELL. 1970. The breeding cycle of the Grey Heron. Ardea 58:171–257.
MONSON, G. 1951. Great Blue Heron killed by bobcat. Wilson Bull. 63:334.
NORTH, P. M. 1979. Relating Grey Heron survival rates to winter weather conditions. Bird Study 26:23–28.
OGDEN J. C., J. A. KUSHLAN AND J. T. TILMANT. 1976. Prey selectivity by the Wood Stork. Condor 78:324–330.
———, ——— AND ———. 1978. The food habits and nesting success of Wood Storks in Everglades National Park in 1974. Nat. Resour. Rept. 16. U.S. National Park Service, Washington, D.C.
OWEN, D. F. 1955. The food of the heron *Ardea cinerea* in the breeding season. Ibis 97:276–295.
———. 1960. The nesting success of the heron *Ardea cinerea* in relationship to the availability of food. Proc. Zool. Soc. London 133:597–617.

Palmer, R. S. 1962. Handbook of North American birds. Vol. 1. Yale Univ. Press, New Haven, Connecticut.

Recher, H. F. and J. A. Recher. 1969a. Comparative foraging efficiency of adult and immature Little Blue Herons *(Florida caerulea)*. Anim. Behav. 17:300–322.

——— and ———. 1969b. Comments on the escape of prey from avian predators. Ecology 49:560–562.

——— and ———. 1972. The foraging behavior of the reef heron. Emu 72:85–90.

Reynolds, C. M. 1979. The heronries census: 1972–77 indices and a review. Bird Study 26:7–12.

Robins, J. D. 1970. Feeding behavior of several aerial foragers after an extended rainy period. Trans. Kansas Acad. Sci. 73:434–438.

Russell, J. K. 1978. Effects of interspecific dominance among egrets commensally following Roseate Spoonbills. Auk 95:608–610.

Ryder, R. A. 1967. Distribution, migration and mortality of the White-faced Ibis *(Plegadis chihi)* in North America. Bird-Banding 38:257–275.

———. 1978. Breeding distribution, movements and mortality of Snowy Egrets in North America. Pp. 197–205 *in* Wading birds (A. Sprunt, IV, J. C. Ogden and S. Winckler, eds.). Natl. Audubon Soc., New York, New York.

Schoener, T. W. 1971. Theory of feeding strategies. Ann. Rev. Ecol. Syst. 2:369–404.

Siegfried, W. R. 1971. Communal roosting of the Cattle Egret. Trans. R. Soc. S. Africa 39:419–443.

———. 1972. Food requirements and growth of Cattle Egrets in South Africa. Living Bird 11:193–206.

———. 1978. Habitat and the modern range expansion of the Cattle Egret. Pp. 315–324 *in* Wading birds (A. Sprunt, IV, J. C. Ogden and S. Winckler, eds.). Natl. Audubon Soc., New York, New York.

Stafford, J. 1971. The heron population of England and Wales, 1928–1970. Bird Study 12:218–221.

Steen, I. and J. B. Steen. 1965. The importance of the legs in the thermoregulation of birds. Act. Physiol. Scand. 63:285–291.

Taylor, R. J. and E. D. Michael. 1971. Predation on an inland heronry in eastern Texas. Wilson Bull. 83:172–177.

Teal, J. M. 1965. Nesting success of egrets and herons in Georgia. Wilson Bull. 77:257–263.

Thompson, D. H. 1978. Feeding areas of Great Blue Herons and Great Egrets nesting within the flood plain of the upper Mississippi River. Proc. Conf. Colonial Waterbird Group 2:202–213.

Urban, E. K. 1974. Breeding of Sacred Ibis *Threskiornis aethiopica* at Lake Shala, Ethiopia. Ibis 116:263–277.

Werschkul, D. F. 1979. Nestling mortality and the adaptive significance of early locomotion in the Little Blue Heron. Auk 96:116–130.

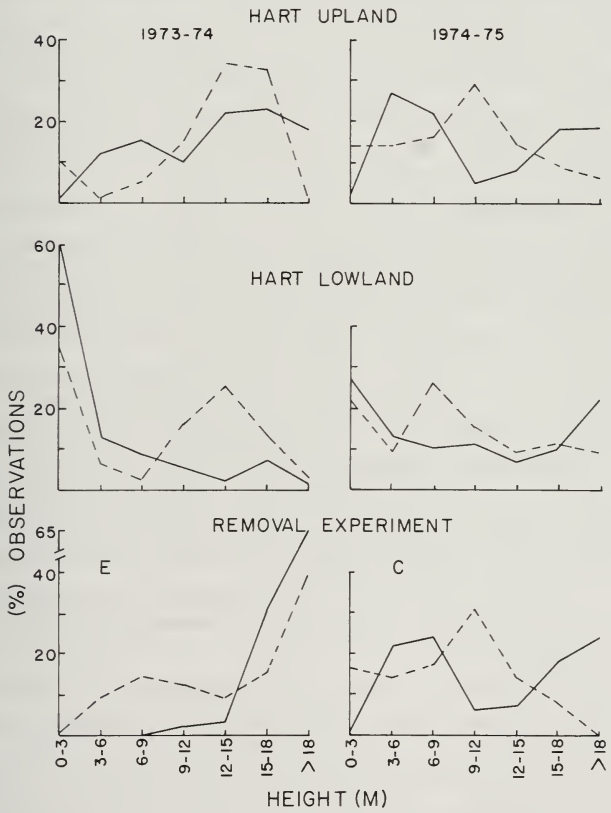
Willard, D. E. 1977. The feeding ecology and behavior of five species of herons in southeastern New Jersey. Condor 79:462–470.

Wolford, J. W. and D. A. Boag. 1971. Food habits of Black-crowned Night Herons in Alberta. Auk 88:435–437.

Woolfenden, G. E., S. C. White, R. L. Mumme and W. B. Robertson, Jr. 1976. Aggression among starving Cattle Egrets. Bird-Banding 47:48–53.

NATIONAL PARK SERVICE, SOUTH FLORIDA RESEARCH CENTER, P.O. BOX 279, HOMESTEAD, FLORIDA 33030. ACCEPTED 30 JULY 1980.

Erratum.— Vol. 92, No. 4. "Intersexual niche partitioning in Downy Woodpeckers" by Joseph B. Williams. Fig. 3, p. 446, should be disregarded and the figure appearing on p. 444 substituted. Fig. 3 caption remains the same. The figure printed below should be substituted for Fig. 2, p. 444. Fig. 2 caption remains the same.



Wilson Bull., 93(2), 1981, pp. 164–188

AGE RATIOS AND THEIR POSSIBLE USE IN DETERMINING AUTUMN ROUTES OF PASSERINE MIGRANTS

C. John Ralph

A principal interest of early students of passerine migration was the determination of direction, location and width of migratory routes. In such studies, it was presumed that an area where the species was most abundant was the main migration route. However, during fall, passerine migrants tend to be silent and inconspicuous, rendering censusing subjective at best. Species also differ in preferred habitat, affecting the results of censuses and the number captured by mist netting. In this study, I used the abundance of migrants with another possible criterion, their age ratios, in order to hypothesize possible migratory routes.

Based upon information about species abundance in different areas, a lively debate sprang up in the past between a school favoring narrow routes and one advocating broad front migration. The former suggested that birds followed topographical features ("leading lines") such as river valleys, coast lines and mountain ranges (Baird 1866, Palmen 1876, Winkenwerder 1902, Clark 1912, Schenk 1922). The latter group proposed that a species migrated over a broad geographical area regardless of topographical features (Gätke 1895; Cooke 1904, 1905; Geyr von Schweppenburg 1917, 1924; Moreau 1927). Thompson (1926) and later Lincoln (1935), suggested that both schools were probably right, depending upon the species involved. Early ornithologists were possibly misled because of the differences between easily observable (and often narrow front), diurnal migration and less obvious, but probably more common, nocturnal movements. A species could participate in both and yet be considered only a narrow front, diurnal migrant.

In the last 50 years, the dichotomy was apparently resolved with narrow routes being generally ascribed to diurnal migrants following topographical features, and broad routes ascribed to migrants moving at night, ignoring topographical features (Moreau 1961, Dorst 1962). This view, however, is by no means unanimous (cf. Van Dobben 1935, Deelder 1949). Indeed, Phillips (1951), King et al. (1965), Clench (1969) and Leberman and Clench (1975) have suggested that populations, as well as different age and sex classes of some nocturnal migrants, follow different routes.

On the basis of radar observations, Drury and Keith (1962) have divided fall nocturnal land bird migrants on the Atlantic coast into 2 groups. They suggest that most migrate southwest on a broad front over land, while a few species fly over water from the Atlantic coast of North America to

South America. Among the passerine migrants, only the Blackpoll Warbler (*Dendroica striata*) is known to use this second route (Nisbet et al. 1963, Nisbet 1970).

The "coastal effect."—Interest in age ratios of birds captured during fall migration has focused on the 85–95% incidence of young of most species on the Atlantic coast (Robbins et al. 1959, Drury and Keith 1962, Murray 1966), as compared to 65–70% inland (Nisbet et al. 1963; Barry 1970; Leberman and Clench 1972, 1973). Similarly, high numbers of young prevail on the Pacific coast (Ralph 1971, Stewart et al. 1974). I shall refer to this high percentage of young as the "coastal effect." In Europe, despite much fieldwork, the coastal effect is reported only in passing by Williamson (1959) and Evans (1968).

King et al. (1965:497), Barry (1970) and Leberman and Clench (1975:10) have suggested that the age classes follow different routes, the adults inland, the young along the coast. In view of the substantial number of young inland, even in species with a coastal effect, this interpretation must be incorrect for most species. Most young migrate inland (Ralph 1975). An alternate hypothesis, that high percentages of young denote the periphery of a species' migration route, is a major thesis of this paper.

Use of age ratios.—The rationale for this latter hypothesis is as follows. I assume that a species' main routes are adaptive and take the birds through the most congenial habitats to the most salubrious wintering grounds. Assume then that individuals straying from main routes (see Ralph 1978) will suffer a higher mortality rate than those following them. The next year, strays either will have perished or perhaps have learned a more appropriate orientation. Therefore, by their second fall migration, relatively few individuals should be wandering from the mainstream of the routes. Those individuals at the periphery of routes should be almost entirely young birds on their first trip.

If the coast (with high percentages of young) is the edge of a route, then areas with relatively low percentages of young should represent the actual routes that the species used. In this study, I document age ratios and abundances of migrants and recognize 5 main patterns.

Age ratios from more than 1 site have been compared in the past, giving a geographical perspective (Drury and Keith 1962; Nisbet et al. 1963; Johnson 1965, 1970, 1973; Stewart et al. 1974; Robbins 1976). These authors had few data from sites at any sufficient distance from coasts, and none postulated routes based on age ratio data.

MATERIALS AND METHODS

Sites and species involved.—Data were obtained from records of mist netting and collections of nocturnal migrants killed by colliding with man-made structures (Table 1 and Fig. 1). Certain sites in Massachusetts (Fig. 2) are located on or near the Cape Cod Peninsula,

TABLE 1

LOCATION AND CHARACTERISTICS OF THE SAMPLING STATIONS USED IN THIS STUDY DURING THE FALL MIGRATION

Location	Distance from coast (km)[a]	Source of data	Dates of operation	Type of operation	Additional information
Coastal					
Monomy Is., Mass.	+130	J. Baird (pers. comm.)	1956–70 (21 Aug.–15 Oct., intermittent)	mist nets	
Manomet, Mass.	+60	this study and K. Anderson et al. (pers. comm.)	1970[b]–71 (entire period) (some 1972–73)	mist nets	Manomet Bird Observatory
Boston, Mass.	0	J. Baird (pers. comm.)	1969–70 (entire period)	nocturnal kills at a building	Prudential Center
Island Beach, N.J.	0	B. Murray (1966, pers. comm.)	1963 (2 Aug.–26 Oct.)	mist nets	
Coastal plain					
Sudbury, Mass.	−35	Howard (1967)	1962–66 (1 Sept.–15 Oct., usually)	mist nets	

TABLE 1
CONTINUED

Location	Distance from coast (km)[a]	Source of data	Dates of operation	Type of operation	Additional information
Littleton, Mass.	−50	J. Baird (pers. comm.)	1966–70 (entire period intermittent)	mist nets	
Boylston, Mass.	−60	Baird (1971, 1972)	1970–72 (entire period)	nocturnal kills at a TV tower	
Ashby, Mass.	−80	this study	1971[b] (entire period)	mist nets	Ashby Bird Observatory
Inland					
Carlisle, Penn.	−160	this study	1973–75[b] (1 Sept.–15 Nov.)	mist nets	Reineman Wildlife Sanctuary
Rector, Penn.	−275	Leberman and Clench (1972–73, pers. comm.)	1961–73 (entire period some later)	mist nets	Powdermill Nature Reserve

[a] + indicates east of the coast; − indicates to the west (inland).
[b] Author supervised or made a major contribution of time to operations.

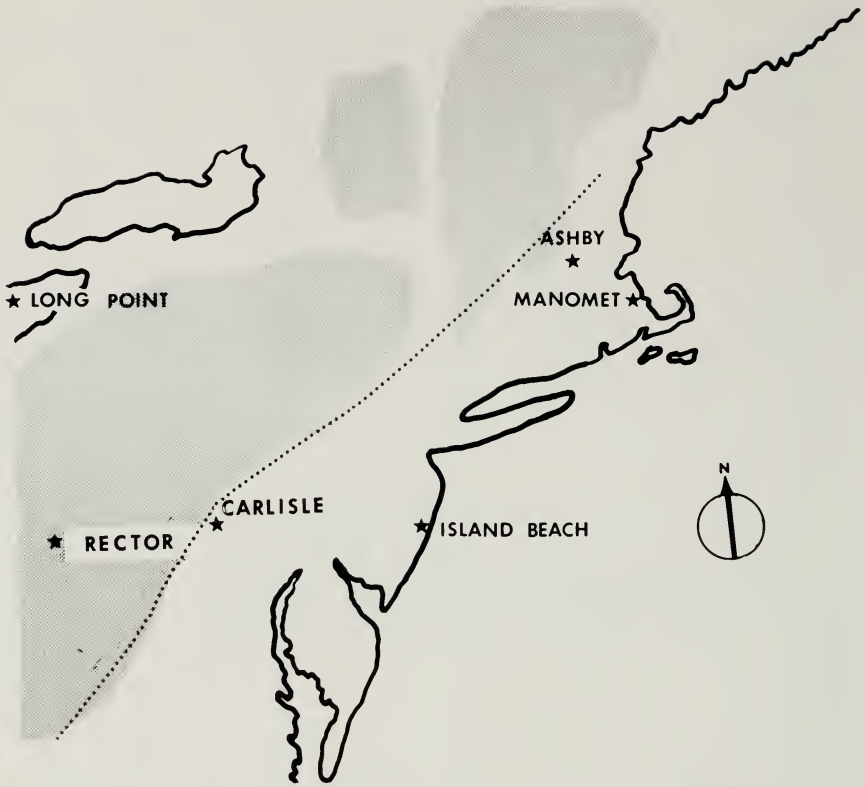


FIG. 1. Map of the northeast United States showing principal sources of data outside of Massachusetts. Shaded areas indicate mountainous regions, and the dotted line indicates the western boundary of the coastal plain.

which extends some 130 km out into the Atlantic. In this study, I consider the Monomoy station to be 130 km beyond the main coast line, Manomet approximately 60 km out, and Boston on the coast line. Carlisle lies at the junction of the coastal plain and the Appalachians and perforce should usually yield age ratios and abundances intermediate between those characteristic of coastal plain stations and those of Rector, the station on the western side of the Appalachians. I considered only those species with samples of $N \geq 20$ in at least 2 locations. On this basis, data for 61 species of autumn migrants (out of a possible 150+) were available, representing 42,219 individuals. The 61 species comprised 90–95% of the passerine migrants.

The period of fall migration was considered to be from 1 August to mid-November. Use of this time period helped to minimize bias caused by including local residents. Some post-breeding wandering occurring in early August is not "true" migration, and usually involves relatively few birds. Such movements are overshadowed by true fall migration (Ralph, unpubl.). Furthermore, many migratory movements begin as early as the first week in August and should be included. Migration occurring after mid-November involves relatively few individuals (Leberman and Clench 1972, 1973, 1975).

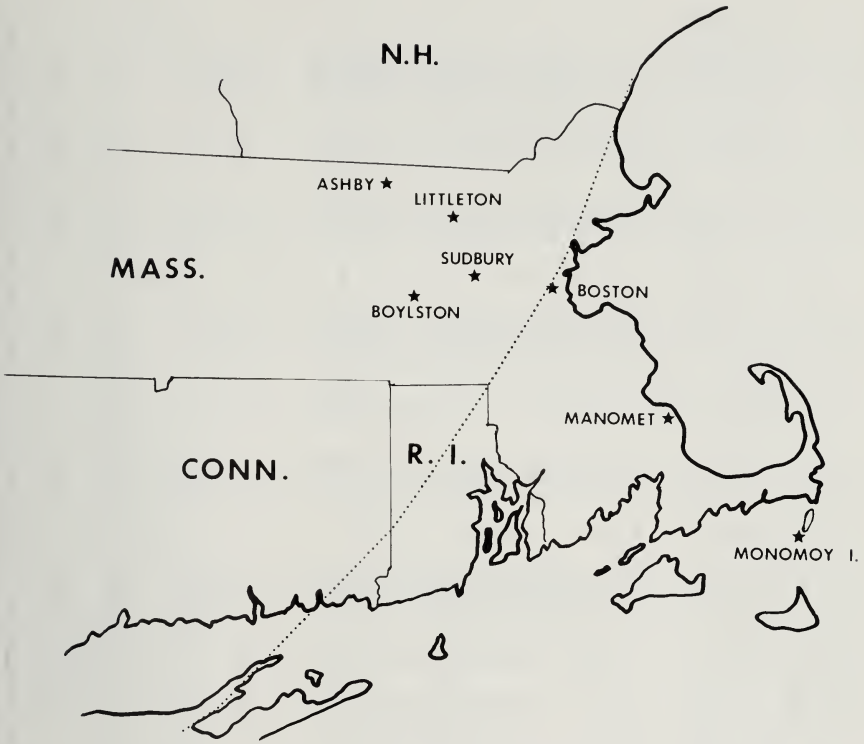


FIG. 2. Map of the stations located in Massachusetts. The dotted line indicates the coast as it is considered in this paper. Stations to the east were considered coastal stations, and those to the west were considered coastal plain stations.

Age ratios, abundances and timing of migration.—Age was usually determined by assessing degree of skull ossification (see Miller 1946, Norris 1961). This technique could be reliably employed through at least mid-November. Age was also determined in a few species on the basis of diagnostic plumage characters (e.g., White-crowned Sparrows [*Zonotrichia leucophrys*]).

Significance levels between percentages of young were calculated using an arcsine transformation (Sokal and Rohlf 1969:607–8). I examined the year-to-year variability of age ratio data at Rector, Pennsylvania, and found that two-thirds of the species vary by less than 10% annually with regard to percentage of young in the sample (Ralph 1975). After 2 years of data collection, more than 95% of the age ratios of all species are within 5% of a long-term (e.g., 10 years) average. I have at least 2 years of data for all but 2 stations; the average was 3.3 years. For rarer species at Rector and Manomet, data from additional years (so labeled in Table 1) were used.

To compare species abundances between sites, I determined the percentage each species comprised of the total number of all passerine birds at that location. At most stations abundance values were calculated on the basis of previously uncaught birds, in order to help eliminate residents. At Rector and Manomet, abundance values were based only on those years in which data from all species were tabulated.

TABLE 2

ASSIGNED ROUTES, PERCENTAGE OF YOUNG, NUMBERS AND PERCENTAGE OF TOTAL OF PASSERINE MIGRANTS

Species name	Diel timing[c]	Rector			Sig-nifi-cance[a]	Carlisle			Sig-nifi-cance[a]	Coastal plain			Sig-nifi-cance[a]	Coast			Win-ter range[a]
		% young	N	% Σ		% young	N	% Σ		% young	N	% Σ		% young	N	% Σ	
Broad front migrants																	
Eastern Phoebe	0.20	0.603	214	0.0091	***	0.119	34	0.0084	***	0.728	77	0.0050	***	1.000	186	0.0063	1
Blue Jay	0.00	0.619	86	0.0021	—	—	16	0.0039	—	0.663	216	0.0139	***	0.810	339	0.0114	1
Red-eyed Vireo	0.95	0.631	1015	0.0225	***	0.786	229	0.0563	*	0.680	195	0.0125	***	0.930	612	0.0206	3
Connecticut Warbler	1.00	0.678	118	0.0034	—	—	4	0.0010	—	0.667	27	0.0017	***	0.950	99	0.0033	3
Mourning Warbler	0.88	0.539	143	0.0030	NS	0.591	44	0.0108	—	—	6	0.0004	—	1.000	82	0.0028	3
Canada Warbler	0.75	0.790	224	0.0051	NS	0.773	122	0.0300	+	0.661	84	0.0054	***	0.965	228	0.0077	3
Purple Finch	0.00	0.717	434	0.0066	NS	0.637	32	0.0079	NS	0.707	33	0.0021	+	0.850	174	0.0059	1
Swamp Sparrow	0.70	0.692	1208	0.0319	***	0.183	21	0.0052	***	0.613	53	0.0034	***	0.940	513	0.0173	1
Dark-eyed (Slate-colored) Junco	0.65	0.432	1814	0.0548	***	0.642	132	0.0324	**	0.747	499	0.0321	***	0.971	858	0.0289	1
Field Sparrow	0.36	0.695	1879	0.0609	NS	0.589	52	0.0128	NS	0.703	64	0.0041	***	0.918	282	0.0095	1
White-throated Sparrow	0.69	0.566	2103	0.0592	***	0.464	361	0.0887	***	0.645	656	0.0422	***	0.916	1445	0.0487	1
Fox Sparrow	0.78	0.508	122	0.0044	—	—	3	0.0007	—	0.541	43	0.0028	***	0.980	152	0.0051	1
Tentative broad front migrants																	
Ruby-crowned Kinglet	0.34	0.401	674	0.0411	***	0.188	245	0.0602	***	0.575	400	0.0257	NS	0.533	169	0.0057	1
Yellow Warbler	0.70	0.780	59	0.0017	—	—	0	0.0000	—	0.800	20	0.0013	+	0.932	236	0.0080	3
Song Sparrow	0.62	0.689	2125	0.0746	NS	0.677	42	0.0103	*	0.825	267	0.0172	NS	0.861	697	0.0235	1
Coastal migrant																	
Red-breasted Nuthatch	0.32	—	0	0.0000	—	—	0	0.0000	—	0.937	30	0.0019	***	0.718	732	0.0247	1
Tentative coastal migrant																	
Black-capped Chickadee	0.00	0.898	303	0.0390	—	—	13	0.0032	—	0.923	562	0.0362	*	0.946	4282	0.1443	1

TABLE 2
Continued

Species name	Diel timing[c]	Rector			Sig-nifi-cance[a]	Carlisle			Sig-nifi-cance[a]	Coastal plain			Sig-nifi-cance[a]	Coast			Win-ter range[a]
		% young	N	% Σ		% young	N	% Σ		% young	N	% Σ		% young	N	% Σ	
Coastal and coastal plain migrant																	
Tennessee Warbler	0.87	0.949	1616	0.0233	—	0.934	56	0.0138	***	0.732	128	0.0082	NS	0.660	97	0.0033	3
Coastal plain migrants																	
Gray Catbird	0.56	0.862	1271	0.0533	***	0.676	253	0.0622	*	0.774	228	0.0147	***	0.940	2149	0.0724	1
American Robin	0.32	0.927	167	0.0071	—	—	10	0.0025	—	0.524	202	0.0130	***	0.926	1016	0.0342	1
Wood Thrush	0.75	0.879	91	0.0035	+	0.743	32	0.0079	NS	0.790	105	0.0068	***	0.949	79	0.0027	3
Hermit Thrush	0.55	0.937	222	0.0073	***	0.674	25	0.0061	NS	0.751	203	0.0131	***	0.942	294	0.0099	1
Swainson's Thrush	0.87	0.875	527	0.0274	***	0.766	173	0.0425	***	0.555	283	0.0182	***	0.935	602	0.0203	3
Gray-cheeked Thrush	0.81	0.827	127	0.0084	+	0.647	23	0.0057	***	0.443	51	0.0033	***	0.916	155	0.0052	3
Veery	0.94	0.938	32	0.0010	**	0.660	32	0.0079	NS	0.591	77	0.0050	***	0.843	204	0.0069	3
Brown Thrasher	0.00	0.821	78	0.0034	—	—	10	0.0025	—	0.516	25	0.0016	**	0.786	103	0.0035	1
Black-and-white Warbler	0.80	0.875	80	0.0025	*	0.643	26	0.0064	—	0.621	310	0.0199	***	0.868	449	0.0151	2
Parula Warbler	0.88	—	10	0.0002	—	—	4	0.0010	—	0.600	117	0.0075	**	0.807	62	0.0021	3
Magnolia Warbler	0.85	0.818	1258	0.0287	***	0.421	140	0.0344	***	0.674	192	0.0124	***	0.919	296	0.0100	3
Black-throated Blue Warbler	0.95	0.912	57	0.0011	—	0.875	49	0.0120	NS	0.802	140	0.0090	***	0.933	270	0.0091	3
Palm Warbler	0.53	0.920	388	0.0129	—	—	5	0.0012	—	0.787	65	0.0042	***	0.988	479	0.0161	2
Ovenbird	1.02	0.875	255	0.0073	***	0.621	69	0.0170	*	0.773	283	0.0182	***	0.925	308	0.0104	3
Northern Waterthrush	0.76	0.722	187	0.0046	NS	0.737	26	0.0064	**	0.430	54	0.0035	***	0.844	532	0.0179	3
Common Yellowthroat	0.95	0.788	1606	0.0487	*	0.643	57	0.0140	NS	0.533	150	0.0097	***	0.782	836	0.0282	2
American Redstart	0.79	0.849	523	0.0123	**	0.685	47	0.0115	NS	0.653	406	0.0261	***	0.968	721	0.0243	3
Scarlet Tanager	0.90	0.900	251	0.0082	***	0.714	65	0.0160	NS	0.702	45	0.0029	***	0.938	113	0.0038	3
Rose-breasted Grosbeak	0.77	0.774	124	0.0061	NS	0.732	80	0.0197	NS	0.589	22	0.0014	**	0.899	50	0.0017	3
Rufous-sided Towhee	0.21	0.791	492	0.0108	***	0.418	62	0.0152	***	0.709	170	0.0109	***	0.910	304	0.0102	1

TABLE 2
Continued

Species name	Diel timing[c]	Rector			Sig-nifi-cance[a]	Carlisle			Sig-nifi-cance[a]	Coastal plain			Sig-nifi-cance[a]	Coast			Win-ter range[a]
		% young	N	% Σ		% young	N	% Σ		% young	N	% Σ		% young	N	% Σ	
Tentative coastal plain migrants																	
Brown Creeper	0.30	0.721	86	0.0015	—	—	0	0.0000	—	0.620	68	0.0044	***	0.819	541	0.0182	1
Yellow-rumped (Myrtle) Warbler	0.82	0.765	1645	0.0464	—	—	18	0.0044	—	0.662	1455	0.0936	***	0.924	3690	0.1243	1
Savannah Sparrow	0.94	—	49	0.0010	—	—	0	0.0000	—	0.610	36	0.0023	***	0.944	714	0.0241	1
Appalachian migrant (Carlisle and west)																	
Least Flycatcher	0.34	0.790	391	0.0249	NS	0.804	44	0.0108	—	—	12	0.0008	—	0.931	131	0.0044	3
Eastern Wood Pewee	0.61	0.856	299	0.0087	NS	0.798	39	0.0096	—	—	10	0.0006	—	0.793	29	0.0010	3
Nashville Warbler	0.76	0.690	393	0.0102	**	0.478	52	0.0128	***	0.896	144	0.0093	**	0.973	111	0.0037	3
Wilson's Warbler	0.65	0.556	306	0.0073	NS	0.591	21	0.0052	*	0.857	21	0.0014	*	0.988	171	0.0058	3
Indigo Bunting	0.72	0.784	365	0.0153	**	0.875	198	0.0486	—	—	7	0.0005	—	—	11	0.0004	3
American Goldfinch	0.00	0.480	1762	0.0671	***	0.589	747	0.1835	+	0.723	45	0.0029	NS	0.686	35	0.0012	1
Tentative Appalachian migrant (Carlisle and west)																	
House Wren	0.30	0.873	221	0.0177	***	0.534	20	0.0049	***	0.929	28	0.0018	NS	0.985	68	0.0023	2
Appalachian migrants (Rector and west)																	
Black-throated Green Warbler	0.83	0.765	372	0.0086	*	0.902	38	0.0093	NS	0.927	121	0.0078	NS	0.967	91	0.0031	2
White-crowned Sparrow	0.64	0.676	105	0.0032	—	—	1	0.0002	—	—	18	0.0012	—	0.918	110	0.0037	1
Lincoln's Sparrow	0.69	0.775	493	0.0174	—	—	13	0.0032	—	0.973	38	0.0024	NS	0.938	81	0.0027	2

TABLE 2
Continued

Species name	Diel timing[c]	Rector % young	Rector N	Rector % Σ	Significance[a]	Carlisle % young	Carlisle N	Carlisle % Σ	Significance[a]	Coastal plain % young	Coastal plain N	Coastal plain % Σ	Significance[a]	Coast % young	Coast N	Coast % Σ	Winter range[a]
Tentative Appalachian migrant (Rector and west)																	
Golden-crowned Kinglet	0.44	0.608	181	0.0100	—	—	13	0.0032	—	0.772	119	0.0077	*	0.870	264	0.0089	1
West of Appalachian migrants (high percentage young at all stations)																	
Yellow-bellied Flycatcher	0.38	0.952	333	0.0080	—	0.929	51	0.0125	—	—	12	0.0008	—	0.955	112	0.0038	3
Solitary Vireo	0.39	0.900	108	0.0019	—	0.930	35	0.0086	NS	1.000	21	0.0014	*	0.932	74	0.0025	2
Cape May Warbler	0.68	0.893	512	0.0084	—	—	9	0.0022	—	0.928	46	0.0030	NS	0.937	559	0.0188	3
Chestnut-sided Warbler	0.92	0.850	200	0.0047	NS	0.771	26	0.0064	NS	0.882	52	0.0033	NS	0.905	63	0.0021	3
Bay-breasted Warbler	0.98	0.921	229	0.0030	NS	0.872	54	0.0133	NS	0.826	66	0.0042	NS	0.843	89	0.0030	3
Western Atlantic migrant																	
Blackpoll Warbler	0.81	0.785	233	0.0082	—	—	3	0.0007	—	0.607	6519	0.4194	***	0.798	2056	0.0693	3
Uncertain routes (species whose routes could not be determined)																	
White-breasted Nuthatch	0.00	—	83	0.0016	—	—	3	0.0007	—	0.846	26	0.0017	NS	0.932	59	0.0020	1
Blackburnian Warbler	0.96	0.952	62	0.0011	—	—	13	0.0032	—	0.834	38	0.0024	NS	0.912	34	0.0011	3
Chipping Sparrow	0.42	0.863[d]	373	0.0073	—	—	14	0.0034	—	0.897	29	0.0019	NS	0.942	94	0.0032	2

[a] Between percentage of young in adjacent areas are: — = insufficient data (N < 20, or not available); NS = not significant ($P > 0.10$); + = not significant ($P < 0.10$); * = $P < 0.05$; ** = $P < 0.01$; *** = < 0.001.

[b] Winter ranges are designated as northernmost area commonly wintering in: 1 = Central Atlantic States; 2 = Southeastern United States; 3 = South of United States.

[c] Diel timing of migration from Ralph (1975) are: 1.02 = most nocturnal; 0.00 = most diurnal (see text for explanation).

[d] Based on 51 individuals.

Each netting station differed from others in vegetation, location of nets, net height and operation schedule. These variables affect the capture rate of certain species; they probably do not significantly affect the age composition. Certainly the pooling of data from several sites and years tends to reduce potential biases from this source. At 2 stations, Carlisle and Ashby, it was possible to use techniques previously described (Ralph 1976) to correct the number of captures for varying number of nets and time of operation. This method provides a somewhat more accurate data set, but does not alter the comparisons between stations.

To define nocturnal and diurnal migrants, an index to the diel timing of migration was determined from data taken at Long Point Bird Observatory, Ontario (Bradstreet and Woodford 1970, Woodford 1970). In this analysis (Ralph 1975), a ratio was calculated between the natural logarithms of the number taken during nocturnal flight at a lighthouse and the number taken during the day at netting and trapping operations. The Ovenbird (*Seiurus aurocapillus*) had the highest ratio (1.02), with 1142 at the lighthouse and 1005 caught in nets and traps. Most Ovenbirds apparently migrate at night. A value approaching 0.00 indicated the most diurnal of the migrants (species with no individuals at the lighthouse were assigned the value 0.00).

Assignment of routes.—I regarded a station to be in the mainstream of a species' migratory route if, compared to other stations: (1) adults of that species were more abundant (i.e., the percentage of young was lower), and (2) the species made up a higher percentage of the total catch of passerine birds. Conversely, a station with a relatively high percentage of young and low abundance of that species was considered to be on the periphery of the species' route. These determinations are, of necessity, subjective. Three factors were weighed in making the determinations: (1) the relative magnitude of differences between age ratios and abundances at different stations, (2) the level of significance of differences between stations, and (3) the sample sizes involved. I gave greater weight to age ratios than to abundances, since I assumed that there would be more site bias in the abundance of a given species.

RESULTS

The coastal effect.—Fifty-two of 59 (88.1%) species ($N \geq 20$) at coastal sites (Table 2) had a higher proportion of young on the coast than at the nearest inland (coastal plain or Carlisle) location with adequate data. Of these, 40 species had a significantly ($P \leq 0.05$) higher percentage of young than the age ratio at the inland location.

Patterns of age ratios and abundances.—Data in Table 2 were grouped according to distance from the coast into 4 general regions. The route taken by a species could encompass one or more regions. I outline below the 5 patterns of age ratios and abundances that emerged in the area under consideration. Additional data from other areas, when available, will undoubtedly alter these assignments. No attempt was made to integrate the information on "known" migratory routes from other publications, as these are usually based on somewhat subjective information.

(1) *Possible broad front migrants.*—A species migrating through the northeastern United States in a general southwesterly direction, regardless of topography, is considered to be a broad front migrant. According to my hypothesis, the percentage of young should be higher and abundance lower on the coast than inland. Twelve species appeared to fit this pattern, 20.0% of the total (Table 2).

Three additional species were tentatively assigned to this pattern, the Ruby-crowned Kinglet (*Regulus calendula*), Yellow Warbler (*Dendroica petechia*) and Song Sparrow (*Melospiza melodia*). Skull ossification is completed in this kinglet somewhat earlier than in most species (Leberman 1970), potentially biasing age data. Therefore, kinglet data from Carlisle, mostly from later in the migratory period, were excluded. The Yellow Warbler (an early migrant) was uncommon at all sites, so I disregarded its absence at Carlisle and classified it in the broad front pattern. A high percentage of young in Song Sparrows prevailed until Carlisle, but the species was abundant on the coastal plain.

(2) *Possible coastal migrants.*—A species concentrating its migration along the coast would be more abundant and have a lower percentage of young there than on the coastal plain and inland. Only the Red-breasted Nuthatch (*Sitta canadensis*) showed this pattern clearly (Table 2).

The Black-capped Chickadee (*Parus atricapillus*) also probably follows this route through the northeast. Although it had high percentages of young at all sites, its exceptional abundance (14% of the total) on the coast, suggests this is the main path. Chickadee populations frequently irrupt, and first-year birds are the ones that move (Ralph, unpubl.), so that they would predominate at all sites. In contrast, the nuthatch, also an irruptive species, had substantial numbers of adults in the coastal migration.

The Tennessee Warbler (*Vermivora peregrina*) appears to use both the coast and the coastal plain. However, the high percentage of young (94.9%) and great abundance at Rector, making up 2.3% of the total catch of all species, suggest that this warbler probably has a major route to the west.

(3) *Possible coastal plain migrants.*—This category includes those species that would avoid both the coast and the Appalachian Mountains. Such species would be most common and have the lowest percentage of young on the coastal plain. They would decline in abundance and increase in percentage of young on the coast and also at Carlisle on the boundary of the coastal plain and the Appalachians (and certainly at Rector). Twenty species (32.8%) were assigned to this group.

An additional 3 species were tentatively regarded as coastal plain migrants. The Brown Creeper (*Certhia familiaris*) showed a relatively low percentage of young at Rector, indicating it may fit the broad front pattern, but its high abundance at the coast, coupled with the relatively low percentage of young on the coastal plain, suggests that its route may lie in the latter area. The Yellow-rumped Warbler (*Dendroica coronata*) was common at Rector, but had a significantly ($P < 0.01$) higher percentage of young there than on the coastal plain. This higher incidence at Rector, in addition to the relative scarcity of this species at Carlisle, indicated its pattern fits the coastal plain one. The Savannah Sparrow (*Passerculus sandwichensis*) is more abundant on the coast than the coastal plain, but

the low percentage of young at the latter location would indicate its route is on the coastal plain.

(4) *Possible Appalachian and west migrants.*—If a route of a species lay in and to the west of the Appalachians, one would expect the species to be most common and have the lowest percentage of young at Rector, on the western side of the Appalachians. Towards the coast, the percentage of young would increase either at Carlisle or the coastal plain, and the species would decline in abundance. Fourteen species (23.0%) appeared to fit this pattern. Six species (possibly 7) apparently had routes west of Carlisle. Three (possibly 4), had a pattern indicating a route west of Rector.

Five additional species were tentatively considered to have a route west of Rector. These were species having equally high percentages of young at all stations. The House Wren (*Troglodytes aedon*) seemingly belonged to this group, with a possible route through the region including Carlisle, where the lowest percentage of young (53.4%) was found. At Rector, the percentage of young was significantly higher (87.3%), indicating that this wren might concentrate its route in the Appalachians, although this cannot be determined from available data.

The Golden-crowned Kinglet (*Regulus satrapa*) had its lowest percentage of young at Rector, suggesting that its main migration route is from here to the west. However, nowhere were very high percentages of young found, and the species may actually be a broad front migrant. As with the Ruby-crowned Kinglet, many young birds had ossified skulls early in the season, so age ratios are not reliable, further compounding the problem.

(5) *Possible western Atlantic migrants (the Blackpoll route).*—Blackpoll Warblers, after apparently pausing on the eastern coastal plain, leave North America and head south over water to tropical America (Nisbet 1970). Their main route thus crosses the coast, explaining the relatively low percentages of young at the coast and on the eastern coastal plain. The lowest percentage of young was on the coastal plain rather than the coast (Table 2). This might be expected because most individuals apparently begin their long flight somewhat inland (Nisbet et al. 1963; Richardson, in press). Most species (70.4%) of migrants wintering south of the United States have more than 90% young at the coast (Table 2). However, a few species, like the blackpoll, had relatively low percentages of young (<85%) at the coast. I will consider these species with those that Drury and Keith (1962) suggested as potential overwater migrants (Table 3). They based their list on subjective impressions of density at Bermuda.

Young make up 79.8% of the blackpolls on the coast, more than 10% below the average for all warbler species (90.4%). Of the species with 80% young along the coast, only 2 are on Drury and Keith's (1962) list (Table

TABLE 3

POSSIBLE WESTERN ATLANTIC MIGRANTS, THEIR ASSIGNED ROUTES, THE PERCENT YOUNG FOUND AT COASTAL STATIONS, AND THE NUMBER KILLED AT TV TOWERS IN FLORIDA AND TENNESSEE IN THE AUTUMN

Species	Assigned route	% young on coast	Number in Florida[2]	Number in Tennessee[2]
Palm Warbler[1]	Coastal Plain	98.4	1944	60
American Redstart[1]	Coastal Plain	96.8	1099	229
Yellow Warbler[1]	Tent. Broad Front	93.2	63	11
Ovenbird[1]	Coastal Plain	92.5	1128	2140
Myrtle Warbler[1]	Tent. Coastal Plain	92.4	1006	16
Black-and-white Warbler[1]	Coastal Plain	86.8	502	362
Northern Waterthrush[1]	Coastal Plain	84.4	484	110
Veery	Coastal Plain	84.3	668	3
Bay-breasted Warbler	App. and W.	84.3	157	409
Parula Warbler[1]	Coastal Plain	80.7	1041	8
Blackpoll Warbler[1]	W. Atlantic	79.8	11	20
Eastern Wood Pewee	App. and W.	79.3	34	3
Common Yellowthroat[1]	Coastal Plain	78.2	3477	97
Tennessee Warbler	Coastal and Coastal Plain	66.0	331	1242

[1] Species in Drury and Keith (1962).
[2] Sources given in text.

3) and 4 are not. Five of Drury and Keith's species—Palm (*Dendroica palmarum*), Yellow-rumped and Yellow warblers, American Redstart (*Setophaga ruticilla*) and Ovenbird—have more than 90% young along the coast. In view of the strong coastal effect which these 5 species show, it seems unlikely that they follow a western Atlantic route.

Species using primarily an overwater route would be expected to be rare in the southeastern U.S. in migration. Indeed, the Blackpoll Warbler largely bypasses the southern states in migration (Nisbet 1970). TV tower kills in Florida (Stoddard and Norris 1967, Taylor and Anderson 1973) and in Tennessee (Laskey 1969a, b) show that of the species in Table 3, only Eastern Wood Pewee (*Contopus virens*), Blackpoll and Yellow warblers are apparently rare in both areas. The pewee may actually be more common but may not be susceptible to nocturnal accidents. The Veery (*Catharus fuscescens*), Yellow-rumped and Parula (*Parula americana*) warblers, relatively uncommon in Tennessee, are common in Florida kills. Their principal route might lie to the east of Tennessee.

Abundance in Bermuda would be a good indicator of birds flying between the northeast and South America, since this island group is almost midway in this flight. Adults should comprise a substantial percentage of

Table 4

Percentage of Young, and the Number Caught, of Warblers and Vireos Captured in Bermuda during the Autumn

Species	Percent young	Number caught	Species	Percent young	Number caught
Black-and-white Warbler	96.4	28	Bay-breasted Warbler	66.7	3
Worm-eating Warbler	100.0	6	Blackpoll Warbler	44.4	234
Swainson's Warbler	100.0	1	Prairie Warbler	100.0	2
Prothonotary Warbler	100.0	9	Palm Warbler	100.0	9
Blue-winged Warbler	100.0	1	Ovenbird	89.5	19
Tennessee Warbler	92.3	13	Northern Waterthrush	100.0	30
Nashville Warbler	83.3	6	Kentucky Warbler	100.0	1
Orange-crowned Warbler	100.0	2	Connecticut Warbler	0.0	2
Parula Warbler	85.7	21	Mourning Warbler	100.0	1
Yellow Warbler	100.0	5	Common Yellowthroat	100.0	24
Magnolia Warbler	100.0	23	Yellow-breasted Chat	100.0	2
Cape May Warbler	100.0	5	Hooded Warbler	100.0	8
Black-th. Blue Warbler	100.0	8	Wilson's Warbler	100.0	1
Myrtle Warbler	100.0	1	Canada Warbler	100.0	1
Black-th. Green Warbler	100.0	5	American Redstart	98.8	87
Blackburnian Warbler	100.0	4	Red-eyed Vireo	100.0	43
Chestnut-sided Warbler	100.0	6	Philadelphia Vireo	100.0	4

birds passing through there. Records of warblers and vireos from occasional mist netting in Bermuda by J. Baird and D. Wingate (pers. comm.) show that only the blackpoll is both common and represented by high numbers of adults (Table 4). Thus, it would appear that only the blackpoll, among passerines, uses an overwater route as its major pathway.

Undetermined routes.—It was not possible to determine the route taken by the White-breasted Nuthatch (*Sitta carolinensis*), Blackburnian Warbler (*Dendroica fusca*) and Chipping Sparrow (*Spizella passerina*). Too few data were available for age ratio assessments, and no coastal effect was found. Perhaps additional capture data would clarify the type of routes for these 3 species.

Association of routes with other species characteristics.—To determine if particular routes were associated with the distance migrated, I divided the species in this study according to the northernmost area in which they are found commonly in winter (Table 2, last column): (1) the central Atlantic states, (2) the southeastern Unites States, or (3) south of the United States. Of all species for which I determined a route, nearly half (48.1%) of those wintering south of the United States are coastal plain migrants (Table 5). One-half of the species wintering in the central Atlantic

TABLE 5

NORTHERNMOST WINTERING AREA OF SPECIES PROBABLY AND POSSIBLY (IN PARENTHESES) ASSOCIATED WITH DIFFERENT ROUTES

Route	Central Atlantic States	Southeastern United States	South of United States	Totals
Broad front	8 (2)	0 (0)	4 (1)	12 (3)
Coastal	1 (1)	0 (0)	1 (0)[a]	2 (1)
Coastal Plain	5 (3)	3 (0)	13 (0)[a]	21 (3)
West of Appalachians	2 (1)	3 (1)	9 (0)	14 (2)
Western Atlantic	0 (0)	0 (0)	1 (0)	1 (0)
Undetermined	1	1	1	3
Totals	17 (7)	7 (1)	28 (1)	61

[a] One species had its route on both the coast and the coastal plain.

states showed a broad front migration pattern, while 5 (31.3%) were coastal plain migrants.

Migrant species using the coastal plain tended to have more individuals migrating at night than those using other routes (Table 2), but not significantly so ($P > 0.10$, Mann-Whitney U-test). The average coastal plain migrant had a diel timing index value of 0.717, while broad front migrants averaged 0.575, and Appalachian and west migrants averaged 0.583.

When I grouped the migrants by taxa and compared their routes, more than half of the warblers (52.4%) used the coastal plain, as did the 6 thrush species (Table 2). These relationships were weak, but significant ($P < 0.05$). No other correlations of routes with taxa were found.

DISCUSSION

Possible causes of the coastal effect.—Evidence marshalled in this paper supports the existence of the "coastal effect" and indicates that a high percentage of young in a local sample indicates that a site is on the edge of the main migration route. I previously discussed some of the hypotheses that have been advanced to explain the coastal effect (Ralph 1971). However, additional published data, as well as this study's thorough documentation of the phenomenon, have shed new light on the hypotheses. They fall into 5 main categories.

(1) *Differential timing of migration.*—This hypothesis explains the coastal effect as an artifact of sampling. Brewster (1887), noting that few adults were collected in autumn, postulated that the post-breeding adults migrated in July before the young and before the collectors were active. Differences between adults and young of about 30 days between peaks of

passage were shown in the Least Flycatcher (*Empidonax minimus*) at Long Point (Hussell et al. 1967, Ely 1970) and in the Western Flycatcher (*E. difficilis*) (Johnson 1973, Stewart et al. 1974). However, Clench (1969) found synchronous migration in *E. minimus* at Rector. Also, few inland data were available for the Western Flycatcher, making conclusions necessarily tentative. Murray (1966) and Leberman and Clench (1973) showed as many as 15 days difference at Rector in average migration dates between adults and young for a few species, including the Red-eyed Vireo (*Vireo olivaceus*) and White-throated Sparrow (*Zonotrichia albicollis*). In most species, however, the age classes migrate more or less in synchrony. Certainly, in no known case (with the possible exception of the Western Flycatcher) is the migration asynchronous enough to explain the coastal effect. That is, it does not appear that adults of any species migrate so early as to be missed by netting beginning in August. Finally, the high percentage of adults of most species at inland locations also precludes Brewster's (1887) explanation, which would require that young predominate at both inland and coastal sites during the latter part of the migration.

Alternatively, perhaps adults fly greater distances without stopping and so would not be captured as often. This hypothesis may obtain for those few species with a high percentage of young at all localities, both coastal and far inland, considered above to be migrating west of the Appalachians. I know of no published discussions for or against this hypothesis.

(2) *Adults overflying the coast.*—In discussing Blackpoll Warblers, Murray (1966) postulated that both adult and young nocturnal migrants regularly stray offshore. Both age classes return to the mainland, with the young stopping at landfall, whereas the adults fly farther inland, perhaps seeking more suitable habitat. Thus, the adults pass over the coast but do not land. This hypothesis requires that any bird offshore at dawn (1) have enough energy reserves, (2) have offshore winds slower than its airspeed, and (3) be able to relocate land. I doubt whether a substantial fraction of birds offshore fulfill these conditions.

Kills of several species of migrants at tall structures contradict Murray's hypothesis. The kills at the Prudential Center on the coast in Boston would likely include adults if they were flying over the coast. However, 90.6% of all birds here were young (N = 427). At the Boylston TV tower, 60 km inland, only 46.6% of the kill were young (N = 682). Apparently, the age composition of migrants in the airspace above the coast is similar to that on the ground. Adults are overflying the coast in much lower proportions than they are overflying inland locations.

(3) *Different routes.*—Clench (1969) postulated that adult Least Flycatchers migrate along the Appalachians (as I found), and the young to the east and along the coast, which was not confirmed by this study. I found

5 species that might have different routes used by different age classes. Yellow-bellied Flycatcher (*Empidonax flaviventris*), Solitary Vireo (*Vireo solitarius*), and Cape May (*Dendroica tigrina*), Chestnut-sided (*D. pensylvanica*) and Bay-breasted (*D. castanea*) warblers. These species had high percentages of young at all stations in the area of study, suggesting that the adults might have a route to the west. However, data are lacking that show a preponderance of adults at any location.

(4) *Learning.*—Drury and Keith (1962) have hypothesized that young on their first autumn flight learn to avoid the hazards (e.g., dehydration and depletion of energy reserves) of an overwater flight. As adults, they do not repeat a route taking them to the coast.

Supporting this hypothesis, migrants offshore have been observed by radar to reorient, at times towards land (Myres 1964, Richardson 1978). Indeed, it appears that there is a mechanism allowing migrants with energy reserves to regain land. Those lacking these reserves would perish. Whether the returning birds could learn from their experience, and not repeat their offshore flight, is problematical.

Although the learning hypothesis has considerable merit, it does require many individuals to experience an offshore flight. The hypothesis may not hold for those beginning their flight near the coast and going southeast offshore within the first few hours of night. (Many individuals also head SSW-SW along the shore.) Since individuals offshore observed by radar do not normally change their direction during the night (Richardson 1975), by dawn they would be too far out to return, given normal energy reserves (e.g., Odum et al. 1961) and a definitely offshore direction. With the northeast-southwest orientation of the eastern U.S. coast, even a southward orientation would lead a bird too far offshore to return. Emlen (1969, 1970) has shown that the orientation of Indigo Buntings (*Passerina cyanea*) is defined at an early age, and thus is probably not easily modified by experience. Finally, nocturnal migrants are often reported far offshore, indicating that some individuals persist in flying offshore, with fatal results.

(5) *Maladaptive orientation.*—Drury and Keith (1962) suggested that "the birds which live to be adults are those inheriting a tendency to move on courses which keep them over the mainland." This suggests that birds surviving to become adults generally move on overland routes that avoid the coast because they have proper orientation (Ralph 1971, 1978), adequate compensation for wind drift (Baird and Nisbet 1960) and/or begin migration under conditions not leading to wind displacement from the normal route (Evans 1968). In contrast, the birds along the coast would be largely immature birds not possessing these abilities, as shown in Ralph (1978). They have been, or will be, exposed to the hazards of overwater flight.

Some data support this explanation. The literature abounds with references to land bird migrants at sea, apparently persisting in flying in directions leading potentially to their death. These include observations from ships at sea (e.g., Sprunt 1931, Buckley 1946, Kuroda 1955, Scholander 1955, Hubbs and Banks 1966, Jenson and Livingstone 1969, Williams et al. 1977), on offshore islands (e.g., Howell 1959; Kuroda 1961, 1964; Ralph 1968) and with radar (Williams et al. 1977). Most critical to this hypothesis is that these birds often appear exhausted and sometimes quite emaciated. This has been quantified on an offshore island by Eliassen and Hjelmtvedt (1958) and on the coast by Murray and Jehl (1964) and Ralph (unpubl.).

Williams et al. (1977) provides evidence for offshore mortality, and they ". . . suggest significant mortality for at least some groups of birds." All of these points argue strongly that many individuals do persist in flights involving offshore directions, often with fatal conclusions.

The first 3 hypotheses discussed above may well account for some of the young along the coast. However, the last two are the most tenable, and in my opinion the last has special merit and is probably the cause of the majority of young that reach the coast. The learning and disorientation hypotheses are not necessarily mutually exclusive. Disoriented young that reach the coast and survive might learn to avoid the coast during subsequent migrations.

Species showing little or no coastal effect.—My analysis suggests that the Blackpoll Warbler is possibly the only passerine species using a route over the western Atlantic. It was the only species with all of the following characteristics: (1) relatively low percentage of young along the coast and in Bermuda, (2) uncommon in both Florida and Tennessee, and (3) relatively abundant in Bermuda.

The relatively low percentages of young along the coast in 7 other species (Table 3), could be explained in one of two ways. One would be that the coast is not actually the edge of the route of these species. These apparent exceptions to the principal generalization of this study could have evolved strategies allowing some individuals to survive, despite a tendency to migrate near or even beyond the coast. Richardson's (1978) radar observations of nocturnal passerines migrating off the Atlantic coast of Canada are particularly relevant to this point. In addition to those flying overland (southwest or west), some fly over water and parallel the coast (southwest or south southwest). At dawn, with following winds, they usually kept that course, probably intersecting shore near Virginia. In contrast, those individuals flying under unfavorable winds with a head or side component often changed direction and flew northwest toward the coast during the morning hours. This strategy would enable some of those flying in a generally southwesterly direction near land to survive. Bay-breasted

and Tennessee warblers (west of the Appalachian migrants) with relatively low percentages of young at the coast and no coastal effect, may use this strategy. A change in flight direction may also be in the repertoire of the other 5 long-distance migrants with relatively low percentages of young along the coast.

Determining routes of migration.—Using age ratios and abundances of birds at a given capture station to hypothesize routes of migration is subject to many potential sources of error. It is not the purpose of this paper to explore them all, but it is my judgment that the effect of these variables is relatively minor and does not affect my basic interpretations of the overall picture to any significant degree.

This study, although essentially restricted to northeastern North America, supports Thompson's (1926) suggestion that some species probably migrate over a broad front, while others may follow more narrow paths. In the area studied, 43% of the species apparently avoid the mountains, channeling their flight down the coastal plain or coast. This group does not appear to be restricted to diurnal migrants, as has been suggested. It seems unlikely that these birds would fly over the Appalachians without being detected there. Habitats in the Appalachian Mountains are rather similar to neighboring, lower areas, and these species would be expected to land if they were present. Few of the coastal plain migrants breed only to the north of this area. Undoubtedly, other populations of these species also have routes to the west of the area of this study.

Independent evolution of routes.—I had expected to find strong relationships between routes and other factors, such as diel timing of migration, taxa and distance to wintering grounds, among others. Only weak relationships were found. Most long-distance migrants moving along the coastal plain are insectivorous. This route is near the stabilizing influence of the ocean, perhaps allowing a more dependable food source than a more inland route. Even a slight temperature differential could be a selective force if, for instance, early frosts occasionally decimated insect populations. Those more hardy bird species wintering in the central Atlantic states, by contrast, apparently tended to be broad front migrants in our area, passing through the slightly colder mountains, as well as the coastal plain.

The lack of an association between routes and other characteristics of migration suggests independent evolution of routes by each species. It also indicates that other aspects, such as timing of migration (on both a seasonal and daily basis), have also evolved independently to meet the particular selective pressures acting on each species.

CONCLUSIONS

These data and the resulting hypotheses will, I hope, stimulate further investigations. Most especially, I would urge that the following avenues of

research and predictions be explored and tested: (1) Accurate age ratio data be accumulated from stations to the south and west of the area in this paper. Far too many banders fail to ensure that 95% of captured birds are accurately aged. (2) The limited recovery data available on passerines should be compiled and published, with due regard to the fact that recoveries are usually of birds which have been selected against. (3) If a banding station is on the edge of a migratory route of a species, individuals there may be of lower weight, and with less fat reserves than in the hypothesized central part of a route. (4) If the hypothesis is correct, quantitative data from offshore ships and from islands, at some distance from a "main" route, should include records of lighter birds. (5) It is logical that mist net capture in an area of a given species should be an accurate assessment of the amount of migration of the species in that area. In this paper I held that, due to site bias, they perhaps are not. Several stations or nets set over a wider area than is usually the case should confirm or deny this supposition.

SUMMARY

Age ratios and abundance of 61 migrant passerine species comprising more than 42,000 birds were analyzed in an attempt to determine patterns of migration. The data were collected at 10 stations from coastal Massachusetts to inland Pennsylvania. Age ratios are thought to be useful in determining routes of migration. The principal criteria for the edge of a species' route are suggested to be a higher proportion of young and a lower density of the species than in other areas. Almost all species in this area fell readily into 1 of 5 patterns that suggest 5 possible routes: (1) immediately along the coast (3 species); (2) on the coastal plain (24 species); (3) west of the Appalachians (17 species); (4) overwater, direct to South America (only the Blackpoll Warbler); and (5) an unconfined, broad front, encompassing the entire area (14 species). For 3 species, no route could be determined.

Almost all species showed the "coastal effect," a higher percentage of young along the coast than elsewhere. By the criteria given, this indicates that the coast is the edge of the migratory route of most species. Most probably the young found near the coast lack some navigational capabilities and are off course; many of them probably perish.

In general, a given route was not strongly associated with either diurnal or nocturnal migration, distance to wintering grounds, or with any genus or family of birds. I speculate that this is evidence that routes have evolved independently in each species.

ACKNOWLEDGMENTS

The dedicated help of many persons made this study possible. I would especially like to acknowledge: Kathleen Anderson, Joseph Hagar, Helen Passano and Ken Youngstrom at Manomet Bird Observatory; Frederic and Evelyn Davis, John Goguen, Michael Stopler, Timothy Terrio and many other volunteers at Ashby Bird Observatory; Ed and Iris Swab, Kevin Hess, Walt Tyler, Carter Atkinson, Dick and Meridith Rhindress, Sherry D. Allshouse, and many other friends and students at Carlisle; and especially Lois Vaughn and Natalie Houghton Harrington who helped far above and beyond the call of duty, both at Ashby and Manomet. Stephen T. Emlen and Richard B. Root provided me with much help during a year spent at Cornell University. W. John Richardson, Jon C. Barlow, Erica H. Dunn, David

F. DeSante, Stephen T. Emlen, L. Richard Mewaldt, Bertram G. Murray, Charles and Sandra G. van Riper, and Francis S. L. Williamson read drafts of this manuscript and contributed helpful advice.

I received financial support from the Frank M. Chapman Memorial Fund of the American Museum of Natural History; the National Institutes of Health; the Smithsonian Institution; Dickinson College; and from F. B. Bang and F. S. L. Williamson, who managed to find ways to support me during lean times. Carol Pearson Ralph helped as a volunteer in Carlisle, a manuscript reader and friend throughout this study. Thanks are inadequate for her help.

LITERATURE CITED

Baird, J. 1971. Mortality of fall migrants at the Boylston television tower in 1970. Chickadee 40:17–21.

———. 1972. Mortality of birds at the Boylston television tower in September 1971. Chickadee 41:20–23.

——— and I. C. T. Nisbet. 1960. Northward fall migration on the Atlantic coast and its relation to offshore drift. Auk 77:119–149.

Baird, S. F. 1866. The distributions and migrations of North American birds. Am. J. Sci. 41:78–90, 337–347.

Barry, J. J. 1970. Differential fall migration. EBBA News 34:55–56.

Bradstreet, M. S. W. and P. S. Woodford. 1970. Nocturnal migration. Pp. 19–23 *in* Long Point Bird Observatory 1960–1969, ten-year report (M. S. W. Bradstreet and G. L. Holroyd, eds.). Long Point Bird Observatory, Ontario.

Brewster, W. 1887. Scarcity of adult birds in autumn. Auk 4:268–269.

Buckley, J. L. 1946. Land birds at sea. Auk 63:440.

Clark, W. E. 1912. Studies in bird migration. Gurney and Jackson, London, England.

Clench, M. H. 1969. Additional observations in the fall migration of adult and immature Least Flycatchers. Bird-Banding 40:238–243.

Cooke, W. W. 1904. Distribution and migration of North American warblers. USDA Biol. Surv. Bull. 18.

———. 1905. Routes of bird migration. Auk 22:1–11.

Deelder, C. L. 1949. On the autumn migration of the Scandinavian Chaffinch (*Fringilla c. coelebs* L.) Ardea 37:1–88.

Dorst, J. 1962. The migrations of birds. Houghton Mifflin Co., Boston, Massachusetts.

Drury, W. H. and J. A. Keith. 1962. Radar studies of songbird migration in coastal New England. Ibis 104:449–489.

Eliassen, E. and I. Hjelmtvedt. 1958. The loss of water in wind drifted migratory birds. Univ. Bergen Arbok Naturv. Rekke. Nr. 11.

Ely, C. A. 1970. Migration of Least and Traill's Flycatchers in west-central Kansas. Bird-Banding 41:198–204.

Emlen, S. T. 1969. The development of migratory orientation in young Indigo Buntings. Living Bird 8:113–126.

———. 1970. Celestial rotation: its importance in the development of migratory orientation. Science 170:1198–1201.

Evans, P. R. 1968. Reorientation of passerine night migrants after displacement by the wind. Br. Birds 61:281–303.

Gätke, H. 1895. Heligoland as an ornithological observatory. David Douglas, Edinburgh, Scotland.

Geyr von Schweppenburg, H. 1917. Vogelzug in der westlichen Sahara. J. Orn. Lpz. 65:43–65.

———. 1924. SO-NW Zugstrasse durch die Sahara. J. Orn. Lpz. 72:102–114.

Howard, D. V. 1967. Five years of mist netting (1962–1966) at Round Hill, Sudbury, Massachusetts. Rec. New Eng. Birds 23:iii–vi.

Howell, T. R. 1959. Land birds from Clipperton Island. Condor 61:155–156.

Hubbs, C. W. and R. C. Banks. 1966. Wandering onto the eastern Pacific Ocean of an eastern North America bird, the Bay-breasted Warbler. Auk 83:680–682.

Hussell, D. J. T., T. Davis and R. D. Montgomerie. 1967. Differential fall migration of adult and immature Least Flycatchers. Bird-Banding 38:61–66.

Jenson, A. C. and R. Livingstone, Jr. 1969. Offshore records of land birds. Kingbird 19:5–10.

Johnson, N. K. 1965. Differential timing and routes of the spring migration in the Hammond Flycatcher. Condor 67:423–437.

———. 1970. Fall migration and winter distribution of the Hammond Flycatcher. Bird-Banding 41:169–190.

———. 1973. Spring migration of the Western Flycatcher, with notes on seasonal changes in sex and age ratios. Bird-Banding 44:205–220.

King, J. R., D. S. Farner and L. R. Mewaldt. 1965. Seasonal sex and age ratios in populations of the White-crowned Sparrows of the race *gambelii*. Condor 67:489–504.

Kuroda, N. 1955. Observations on pelagic birds of the northwest Pacific. Condor 57:290–300.

———. 1961. The oversea crossings of land birds in the western Pacific. Misc. Rept. Yamashina's Inst. Ornith. and Zool. 3:47–53.

———. 1964. A survey of seabirds of Teuri Islands, Hokkaido, with notes on land birds. Misc. Rept. Yamashina's Inst. Ornith. and Zool. 3:363–383.

Laskey, A. R. 1969a. T.V. tower casualties at Nashville in autumn 1968. Migrant 40:25–26.

———. 1969b. Autumn 1969. T.V. tower casualties at Nashville. Migrant 40:79–80.

Leberman, R. C. 1970. Pattern and timing of skull pneumatization in the Ruby-crowned Kinglet. Bird-Banding 41:121–124.

——— and M. H. Clench. 1972. Bird-Banding at Powdermill, 1971. Res. Rept. No. 30, Carnegie Museum.

——— and ———. 1973. Bird-Banding at Powdermill, 1972. Res. Rept. No. 31, Carnegie Museum.

——— and ———. 1975. Bird-Banding at Powdermill, 1974. Res. Rept. No. 36, Carnegie Museum.

Lincoln, F. C. 1935. The migration of North American birds. USDA Circ. No. 363.

Miller, A. H. 1946. A method of determining the age of live passerine birds. Bird-Banding 17:33–35.

Moreau, R. E. 1927. Migration as seen in Egypt. Ibis (12)3:443–468.

———. 1961. Problems of Mediterranean-Saharan migration. Ibis 103a:373–427, 580–623.

Murray, B. G., Jr. 1966. Migration of age and sex classes of passerines on the Atlantic coast in autumn. Auk 83:352–360.

——— and J. R. Jehl, Jr. 1964. Weights of autumn migrants from coastal New Jersey. Bird-Banding 35:253–263.

Myres, M. T. 1964. Dawn ascent and reorientation of Scandinavian thrushes (*Turdus* spp.) migrating at night over the northeastern Atlantic Ocean in autumn. Ibis 106:7–51.

Nisbet, I. C. T. 1970. Autumn migration of the Blackpoll warbler: evidence for long flight provided by regional survey. Bird-Banding 41:207–240.

———, W. H. Drury, Jr. and J. Baird. 1963. Weight-loss during migration. Pt.1. Deposition and consumption of fat by the Blackpoll Warbler *Dendroica striata*. Bird-Banding 34:107–138.

Norris, R. A. 1961. A modification of the Miller method of aging live passerine birds. Bird-Banding 32:55–57.

Odum, E. P., C. E. Connell and H. L. Stoddard. 1961. Flight energy and estimated flight ranges of some migratory birds. Auk 78:515–527.

Palmen, J. A. 1876. Uber die Zugstrassen der Vogel. Leiden.

Phillips, A. R. 1951. Complexities of migration: a review. Wilson Bull. 63:129–136.

Ralph, C. J. 1968. Migrants on the Farallon Islands, 1853–1967. Pt. Reyes Bird Obs. Bull. 9:2–7.

———. 1971. An age differential of migrants in coastal California. Condor 73:243–246.

———. 1975. Age ratios, orientation, and routes of land bird migrants in the northeastern United States. Sc.D. thesis, Johns Hopkins Univ., Baltimore, Maryland.

———. 1976. Standardization of mist net captures for quantification of avian migration. Bird-Banding 47:44-47.

———. 1978. The disorientation and possible fate of young passerine coastal migrants. Bird-Banding 49:237–247.

Richardson, W. J. 1975. Bird migration over southeastern Canada, the western Atlantic, and Puerto Rico: a radar study. Ph.D. thesis. Cornell Univ., Ithaca, New York.

———. 1978. Reorientation of nocturnal landbird migrants over the Atlantic Ocean near Nova Scotia in autumn. Auk 95:717–732.

———. Autumn landbird migration over the western Atlantic Ocean as evident from radar. *In* Proc. 17th Int. Ornithol. Congr., Berlin, West Germany. In Press.

Robbins, C. S., D. Bridge and R. Feller. 1959. Relative abundance of adult male redstarts at an inland and a coastal locality during fall migration. Maryland Birdlife 15:23–25.

———. 1976. Atlantic flyway review—region V. N. A. Bird Bander 1:75–77.

Schenk, J. 1922. Bericht uber die ungarischen Vogelberingungen in den Jahren 1920–22. Aquila 29:65–104.

Scholander, S. I. 1955. Land birds over the western north Atlantic. Auk 72:225–239.

Sokal, R. R. and F. J. Rohlf. 1969. Biometry. W. H. Freeman & Co., San Francisco, California.

Sprunt, A., Jr. 1931. Certain land birds observed at sea. Auk 48:133–134.

Stewart, R. M., L. R. Mewaldt and S. Kaiser. 1974. Age ratios of coastal and inland fall migrant passerines in central California. Bird-Banding 45:46–57.

Stoddard, H. L., Sr. and R. A. Norris. 1967. Bird casualties at a Leon County, Florida T.V. Tower. Bull. Tall Timbers Res. Sta. No. 8.

Taylor, W. K. and B. H. Anderson. 1973. Nocturnal migrants killed at a central Florida T.V. tower: autumns 1969–1971. Wilson Bull. 85:42–51.

Thompson, A. L. 1926. Problems of bird-migration. Houghton Mifflin Co., Boston, Massachusetts.

Van Dobben, W. H. 1935. Vogelstrek over Nederland II. Org. Club Ned Vogelk. 7:143–173.

Williams, T. C., J. M. Williams, L. C. Ireland and J. J. Teal. 1977. Autumn bird migration over the western North Atlantic Ocean. Am. Birds 31:251–267.

Williamson, K. 1959. The September drift-movements of 1956 and 1958. Br. Birds 52:334–377.

Winkenwerder, H. A. 1902. The migration of birds with special reference to nocturnal flight. Bull. Wisconsin Nat. Hist. Soc. 2:177–263.

Woodford, P. S. 1970. Banding summary. Pp. 5–11 *in* Long Point Bird Observatory 1960–1969, ten-year report (M. S. W. Bradstreet and G. L. Holroyd, eds.). Long Point Bird Observatory, Ontario.

Appendix A

Scientific Names of Species in Tables Not Mentioned in Text

Eastern Phoebe (*Sayornis phoebe*)
Blue Jay (*Cyanocitta cristata*)
Gray Catbird (*Dumetella carolinensis*)
Brown Thrasher (*Toxostoma rufum*)
American Robin (*Turdus migratorius*)
Wood Thrush (*Catharus mustelina*)
Hermit Thrush (*C. guttata*)
Swainson's Thrush (*C. ustulata*)
Gray-cheeked Thrush (*C. minima*)
Philadelphia Vireo (*Vireo olivaceus*)
Black-and-white Warbler (*Mniotilta varia*)
Prothonotary Warbler (*Protonotaria citrea*)
Swainson's Warbler (*Limnothylypis swainsonii*)
Worm-eating Warbler (*Helmitheros vermivorus*)
Nashville Warbler (*Vermivora ruficapilla*)
Blue-winged Warbler (*V. pinus*)
Orange-crowned Warbler (*V. celata*)
Magnolia Warbler (*Dendroica magnolia*)
Black-throated Blue Warbler (*D. nigrescens*)
Black-throated Green Warbler (*D. virens*)
Prairie Warbler (*D. discolor*)
Northern Waterthrush (*Seiurus noveboracensis*)
Kentucky Warbler (*Oporornis formosus*)
Mourning Warbler (*O. philadelphia*)
Connecticut Warbler (*O. agilis*)
Common Yellowthroat (*Geothlypis trichas*)
Yellow-breasted Chat (*Icteria virens*)
Wilson's Warbler (*Wilsonia pusilla*)
Hooded Warbler (*W. citrina*)
Canada Warbler (*W. canadensis*)
Scarlet Tanager (*Piranga olivacea*)
Rose-breasted Grosbeak (*Pheucticus ludovicianus*)
Purple Finch (*Carpodacus purpureus*)
American Goldfinch (*Spinus tristis*)
Rufous-sided Towhee (*Pipilo erythrophthalmus*)
Dark-eyed Junco (*Junco hyemalis*)
Field Sparrow (*Spizella pusilla*)
Fox Sparrow (*Passerella iliaca*)
Lincoln's Sparrow (*Melospiza lincolnii*)
Swamp Sparrow (*M. georgiana*)

INSTITUTE OF PACIFIC ISLANDS FORESTRY, U.S. FOREST SERVICE, 1151 PUNCHBOWL STREET, HONOLULU, HAWAII 96813. ACCEPTED 8 JULY 1980.

Wilson Bull., 93(2), 1981, pp. 189–195

WEATHER, MIGRATION AND AUTUMN BIRD KILLS AT A NORTH FLORIDA TV TOWER

Robert L. Crawford

Most accounts of nocturnal accidents to migrating birds emphasize occasional large kills and the bewildered behavior of birds encountering towers and lights in fog and overcast weather (Weir 1976, Avery et al. 1978). Tower kills are rarely compared to weather and migration on a daily basis (Avery et al. 1977), probably because few towers are checked for dead birds regularly. Possibly unique in this respect is the WCTV tower in northwest Florida where daily checks have been made since 1955 (Stoddard 1962, Stoddard and Norris 1967, Crawford 1974). This paper uses data from the WCTV tower to determine the influence of weather on autumn bird kills at the WCTV tower and relates these to other migration studies in the southeastern United States.

METHODS

Stoddard and Norris (1967) described the 308 m WCTV tower and its 14-ha cleared site located on Tall Timbers Research Station, Leon Co., Florida. Data on file at Tall Timbers include daily logs of dead birds (primarily passerines) and, for the years 1955–1967, maps of the tower grounds locating the dead birds as they were found on most mornings with ≥ 5 birds. I classified each night (24 August–15 November, 1962–1966) for the presence or absence of north winds, clouds and rain. Local climatological data sheets (U.S. Dept. Commerce) for Tallahassee, Florida, 33 km SW of the WCTV tower provide readings of sky cover, wind and rain at 1- or 3-h intervals for each night (dates herein are the mornings on which the birds were found; weather readings used were at 19:00 and 22:00 the day before and at 01:00, 04:00 and 07:00 the morning of the kill). Cloud data, expressed in tenths of sky covered by all types of clouds, were averaged; nights with a value of ≥4 were classified cloudy except that all nights with rain were considered cloudy. Nights with ≥2 wind readings >270° and <90° I classified for the north winds. Groups of nights with different weather conditions were compared for their numbers of birds with a Kruskal-Wallis test followed by Dunn's procedure for nonparametric multiple comparisons (Hollander and Wolfe 1973:115–120, 125) with significance at the $P < 0.05$ level.

RESULTS

In the 5 autumn periods (N = 420 nights), 8123 birds were killed (Table 1). Nights with north winds (N = 313, 74.5%) accounted for 6744 birds (83%) and nights with south winds (N = 107, 25.5%) had 1379 dead birds (17%). Two hundred and fourteen nights were classified cloudy (50.9%) and these accounted for 6686 birds (82.3%); the 206 clearer nights had only 1437 birds killed (17.7%). Birds were killed on all but 32 of the 420 nights (7%); one-half of these were south-wind nights (although only one-quarter of the nights were classified for south winds) and 22 (68%) were

Table 1

Bird Kills and Weather Conditions at the WCTV Tower: Autumns 1962–1966

Nights with		No clouds A	Clouds B	Clouds and rain C
North winds	No. nights	162	110	41
	No. birds	1326	3427	1991
	$\bar{x} \pm SD$	8.19 ± 25.29	32.06 ± 84.22	48.56 ± 91.15
	Nights with 0	12	4	0
	Sig. dif.[a] from	B, C, D, F	A, D, E	D, E, A
	Not from	E	C, F	F, B
		D	E	F
South winds	No. nights	44	43	20
	No. birds	111	715	553
	$\bar{x} \pm SD$	2.52 ± 3.73	16.62 ± 25.63	27.65 ± 30.17
	Nights with 0	10	5	1
	Sig. dif. from	A, B, C, E, F	B, C, D, F	A, D, E
	Not from	none	A	B, C

[a] $P < 0.05$, Kruskal-Wallis H-value = 103.141 ($P < 0.0005$).

classified as clear. Nights with clear skies and north winds resulted in more birds killed than those with clear skies and south winds but neither equalled the number killed with cloudy skies and north winds. Nights with cloudy skies and south winds had more birds killed than those nights with clear skies and south winds but neither had as great an effect as cloudy skies and north winds. There were no significant differences among groups classified for north winds and clouds, north winds, clouds and rain, and south winds, clouds and rain.

On 36 nights, more than 50 birds were killed; the largest kill was on 19 September 1962 (N = 828) and 10 other nights exceeded 100 birds. All but 2 of the nights with more than 50 birds were associated with cold-front passage (14 October 1964, with 57 birds and 4 September 1966, with 65 birds were not). Cold fronts, the leading edges of cold air masses, are often preceded by south winds and clouds in the vicinity of the WCTV tower. As fronts near the site, storms and rain may occur and then the winds shift to the north. During these conditions the largest kills at WCTV occur. The 2 nights with large kills that were not associated with the passage of cold fronts had clouds and north winds nonetheless. During these 5 autumns about 20 fronts passed the WCTV tower vicinity and did not result in kills of over 50 birds, although they regularly resulted in kills of 15–30 birds. Usually these fronts came through 2–4 days after another front, had relatively clear skies along their leading edges, or were early in the season.

DISCUSSION

The WCTV tower data show 4 consistant patterns: (1) kills occur virtually every night in autumn, (2) kills result during south winds as well as north winds, but north winds result in greater kills than south winds, (3) large kills usually result during the passage of cold fronts, and (4) overcast skies affect the number of birds killed whether with north or south winds. Except for the last, the effects of clouds, the characteristics of autumn kills at the WCTV tower are also those of passerine migration in the southeastern U.S., according to radar and direct-visual studies.

Able (1972, 1973) monitored night migration flights in autumn at Lake Charles, Louisiana and at Athens, Georgia. He recorded migration flights every night, but flights with north winds were greater than those with south winds: 70.5% of the migration volume he recorded at Athens was with north winds. Heaviest flights were with cold-front passage, but often large flights were with north winds not associated with a front, especially if several days had passed with no front. Buskirk (1968) watched incoming flights of autumn migrants in Yucatán; migrants arrived daily but large flights only occurred when cold fronts reached the northern waters of the Gulf of Mexico. Able (1972) noted a similar pattern in departing autumnal migrants from Louisiana and Richardson (1978:239) found this to be a pattern typical of migrants departing over water for long flights. Inland, however, large migration flights in the eastern U.S. seem dependent on synoptic conditions (north winds and a drop in temperature) that are usually present with the passage of a cold front but are not unique thereto (Graber and Cochran 1960, Hassler et al. 1963, Able 1973).

During intervals between fronts, the southeastern U.S. experiences southerly air flows but frontal passage brings colder, northerly winds rather abruptly (Able 1972). Observations that flights with north winds are greater than those with south winds suggest that a pool of physiologically prepared migrants accumulates in the presence of southerly winds. Frontal passage brings north winds and these apparently stimulate a large flight of migrants. At a given site, mass movements continue for 2–3 nights and then decline as the numbers of prepared migrants are fewer or as weather conditions become less favorable. These events are repeated every few days during autumn with the passage of fronts (Able 1973, Alerstam et al. 1973, Weir 1976).

Fig. 1 illustrates this sequence. Between 4 and 25 September 1965, no front passed over the WCTV site and during most of the interval a warm high-pressure center dominated the eastern U.S. A warm front went to Hudson Bay and the southerly flow of warm air precluded mass flights; a large pool of migrants was assembled for the next front which reached the WCTV vicinity on 24 September. The front stalled as it neared the tower;

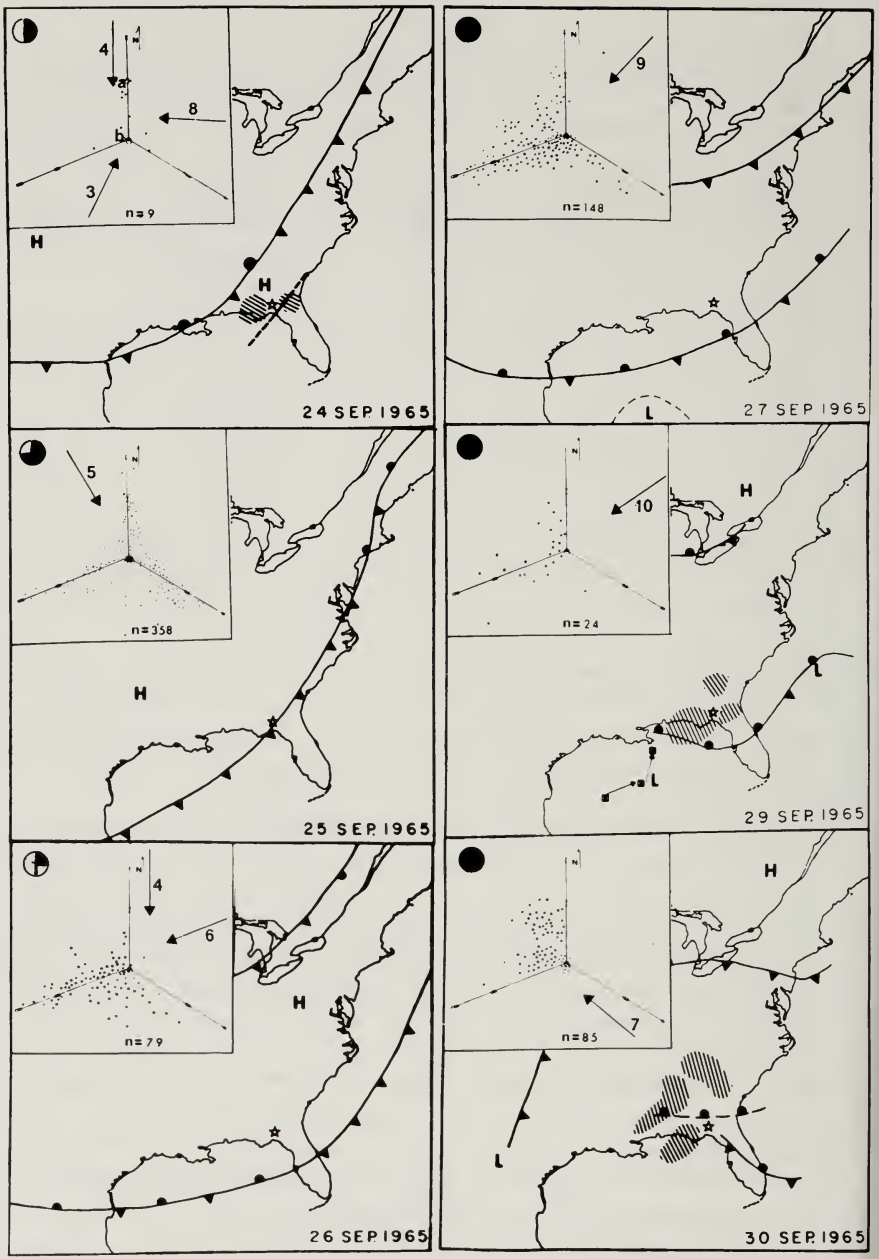


FIG. 1. Surface weather maps (at 01:00) for 24–30 September 1965, and (inserts) WCTV tower maps locating dead birds (dots) and the tower's 3 systems of guy-wires (scale on 24 September map points a–b:116 m). Arrows show predominant winds and speed in knots; partially or completely filled circles indicate amount of overcast; N = number of birds. Rain (hatched areas) is indicated on the weather maps only for the WCTV vicinity (star).

a warm high-pressure center northeast of WCTV and a squall line produced stormy, rainy weather with shifting winds which are conditions possibly not ideal for migration. By 25 September the high-pressure center behind the front moved eastward bringing clearing skies north of the WCTV tower and northwest winds which initiated a mass movement of birds. By 26 September, the center of the high had moved northeast and at WCTV the winds came from the north and northeast. By 27 September, the front was stationary 300 km south of WCTV and northeast winds continued to move birds in large numbers. A low-pressure storm began to develop in the mid-Gulf. No WCTV map is available for 28 September when 32 birds were killed under overcast skies with northeast winds; after 3 days of massed flights, the numbers of birds aloft began to decline. By 29 September, the low-pressure center in the Gulf became Tropical Storm Debbie and tracked towards the mouth of the Mississippi River. The storm created southerly winds and rain along the northeast Gulf coast but at WCTV winds were still northeast into the rain. On 30 September, Debbie went ashore and dissipated; a warm frontogenesis began north of WCTV; rain, overcast and southeast winds prevailed at the tower site. Richardson (1978:261) noted that "reverse flights," with winds contrary to the expected direction of autumn migration, are often associated with the approach of such a low-pressure area as Debbie. Other large kills at WCTV with southerly winds were usually ahead of a front oriented SW–NE, or behind a front with local wind shifts. Lowery and Newman (1966:281) and Able (*in* Bagg 1971:22) noted large autumnal flights with southerly winds under similar circumstances.

The regular association of large kills and cold front passage at WCTV can be attributed to mass movement of birds initiated by the north winds behind the fronts and the presence of cloudy, sometimes stormy weather often along the fronts. Birds encountering these inclemencies on night migration flights may experience north or south winds at the edge and this may account for the lack of significant difference between the night groups C and F (Table 1); they are essentially the same situation.

Apparently clouds are a major factor in tower kills. Weir (1976) and Avery et al. (1978) summarized avian mortality in migration; papers they listed regularly referred to overcast during the kills. Avery et al. (1977), in a thorough study of tower kills in North Dakota, found 70% of their autumn casualties after cloudy nights. Clouds may affect the birds in 2 ways. First, in the southeast U.S. birds generally fly at lower altitudes under overcast (Able 1970); this behavior may simply bring more birds into the range of a tower. Second, the bewildered behavior of birds around lights apparently occurs even without fog or precipitation because light is refracted by a greater number of minute moisture droplets in the air during overcast. Avery et al. (1976) considered Graber's (1968) explanation of the

phenomenon most appropriate: birds enter the illuminated area of a tower and are reluctant to leave; they mill around and many are killed by hitting the tower, guy wires, or other birds. The attraction to the lighted area is limited to the immediate vicinity of the tower; the birds are not drawn from a considerable distance. Herbert (1970) and Gochfeld (1973) discussed this behavior in birds and the effect has been recorded for a variety of lighted situations under overcast (Crawford 1974).

The high percentage of nights with overcast (50.9%) at WCTV may be because of the close proximity of the Gulf of Mexico (76 km S); warm, moist, marine air forms convection clouds and storm systems along cold fronts. If overcast is as important as it seems to the production of tower kills then towers in areas prone to cloudy conditions during migration may kill more birds than towers in areas where clear skies prevail. If the experiences from the WCTV tower are applicable elsewhere, however, birds will be killed nearly every night during autumn migration, even under clear skies. Large kills will be predictable and consistent with migration volume but the smaller day-to-day kills may not be noticed because of the activities of scavenging predators or the condition of the grounds (Crawford 1971, 1974, 1976).

SUMMARY

Autumn bird kills at the 308 m WCTV tower in northwest Florida during 1962–1966 were strongly associated with north winds and overcast. Nights with north winds (N = 313, 74.5% of total) accounted for 6744 (83%) dead birds; south-wind nights (N = 107, 25.5%) had 1379 (17%) birds. Cloudy nights (N = 214, 50.9%) had 6686 (82.3%) birds killed; non-cloudy nights (N = 206, 49.1%) had 1437 (17.7%) dead birds. Large kills were usually associated with the passage of a cold front, but birds were killed on all but 32 (7%) of the nights. The data seem consistent with radar and direct visual studies of migration in the southeastern U.S.

ACKNOWLEDGMENTS

W. Wilson Baker, Harriett Knowles, Lucinda Peace, Henry M. Stevenson, Noel O. Warner and Lynn Wiese helped in various stages of the preparation of the paper. Steve Rathbun advised on statistical analysis and Alvan A. Karlin helped prepare the figure. Referees W. J. Richardson and S. A. Gauthreaux, Jr. strengthened and clarified an earlier version of the paper with valuable suggestions. Herbert L. Stoddard, Sr., and Robert A. Norris gathered the original data.

LITERATURE CITED

Able, K. P. 1970. A radar study of the altitude of nocturnal passerine migration. Bird-Banding 41:282–290.

———. 1972. Fall migration in coastal Louisiana and the evolution of migration patterns in the Gulf region. Wilson Bull. 84:231–242.

———. 1973. The role of weather variables and flight direction in determining the magnitude of nocturnal bird migration. Ecology 54:1031–1041.

Alerstam, T., A. Lindgren, S. G. Nelsson and S. Ulfstrand. 1973. Nocturnal passerine migration and cold front passages in autumn—a combined radar and field study. Ornis Scand., Fenn. 4:103–111.

Avery, M. [L.], P. F. Springer and J. F. Cassel. 1976. The effects of a tall tower on nocturnal bird migration—a portable ceilometer study. Auk 93:281–291.

———, ——— and ———. 1977. Weather influences on nocturnal bird mortality at a North Dakota tower. Wilson Bull. 89:291–299.

———, ——— and N. S. Dailey. 1978. Avian mortality at man-made structures: an annotated bibliography. Biol. Ser. Prog., FWS/OBS–78/58, U.S. Dept. Interior.

Bagg, A. M. 1971. The changing seasons. Am. Birds 25:15–23.

Buskirk, W. H. 1968. The arrival of trans-Gulf migrants on the northern coast of Yucatán in fall. M.S. thesis, Louisiana State Univ., Baton Rouge, Louisiana.

Crawford, R. L. 1971. Predation on birds killed at TV tower. Oriole 36:33–35.

———. 1974. Bird casualties at a Leon County, Florida TV tower: October 1966–September 1973. Bull. Tall Timbers Res. Sta. 18:1–27.

———. 1976. Some old records of TV tower kills from southwest Georgia. Oriole 41:45–51.

Graber, R. R. 1968. Nocturnal migration in Illinois—different points of view. Wilson Bull. 80:36–71.

——— and W. F. Cochran. 1960. Evaluation of an aural record of nocturnal migration. Wilson Bull. 72:253–273.

Gochfeld, M. 1973. Confused nocturnal behavior of a flock of migrating Yellow Wagtails. Condor 75:252–253.

Hassler, S. S., R. R. Graber and F. C. Bellrose. 1963. Fall migration and weather, a radar study. Wilson Bull. 75:56–77.

Herbert, A. D. 1970. Spatial disorientation in birds. Wilson Bull. 82:400–419.

Hollander, M. and D. A. Wolfe. 1973. Nonparametric statistical methods. J. Wiley & Sons, New York, New York.

Lowery, G. H., Jr. and R. J. Newman. 1966. A continentwide view of migration on four nights in October. Auk 83:547–586.

Richardson, W. J. 1978. Timing and amount of bird migration in relation to weather: a review. Oikos 30:224–272.

Stoddard, H. L., Sr. 1962. Bird casualties at a Leon County, Florida TV tower, 1955–1961. Bull. Tall Timbers Res. Sta. 1:1–94.

——— and R. A. Norris. 1967. Bird casualties at a Leon County, Florida TV tower: an eleven-year study. Bull. Tall Timbers Res. Sta. 8:1–104.

Weir, R. D. 1976. Annotated bibliography of bird kills at man-made obstacles: a review of the state of the art and solutions. Dept. Fisheries and Environment, Canadian Wildl. Serv., Ontario Region.

TALL TIMBERS RESEARCH STATION, RT. 1, BOX 160, TALLAHASSEE, FLORIDA 32312. ACCEPTED 1 MAY 1980.

Wilson Bull., 93(2), 1981, pp. 196–206

CLIMATIC INFLUENCES ON PRODUCTIVITY IN THE HOUSE SPARROW

W. Bruce McGillivray

The selection of a poor nesting site could drastically lower the breeding success of a pair of birds. Given particular habitat requirements, selection should constrain nest structure and nest-site to characteristic types. This conclusion has been tacitly assumed by biologists and field naturalists who were aware that nest-sites were not randomly scattered but associated with species specific habitat and structural configurations. However, several studies have demonstrated intraspecific variation in nest-site choice and subsequent differences in productivity among sites (Orians 1961, Robertson 1973, Will 1973, Caccamise 1977, Murphy 1977, Anderson 1978).

Cody (1971) suggested that predation is the single greatest cause of reproductive failure in most species of birds. Predation was also considered to be an important factor in the distribution of nests (Horn 1968, Lack 1968), with higher productivity in the best concealed or least accessible nests. Climate is accorded a role in nesting success but usually only indirectly as a determinant of food abundance. Severe weather can have a major effect on reproductive output at a site (Mitchell et al. 1973) by damaging or destroying nests. Birds thus could be expected to construct nests to reduce the detrimental influence of weather (Collias 1964, Austin 1974, Inouye 1976, Schaeffer 1976, Mertens 1977); this tendency would be strong if weather was the major cause of reproductive failure. This situation obtains for a population of House Sparrows (*Passer domesticus*) on a ranch near Calgary, Alberta. Human activity, plus thick blue spruce (*Picea pungens*) foliage combine to reduce egg and nestling loss to predators (Black-billed Magpies [*Pica pica*] and cats) to negligible levels (Murphy 1977, McGillivray 1978). The large population of House Sparrows provided an opportunity to assess variation in reproductive performance associated with nest-site differences. This study was undertaken to determine if weather-related factors could influence the nest placement and reproductive performance of House Sparrows.

MATERIALS AND METHODS

Study site.—The study area was on a ranch located 8 km east of Calgary, Alberta (51°05′N, 113°50′W). The 146 nests found were in 2 rows of blue spruce originally grown as windbreaks. Generally, several thousand bushels of grain were stored on the ranch and high protein feed was always available. Two heated barns supplied shelter for the sparrows in inclement weather and throughout the winter. Twenty-four nest boxes were installed on the sides of farm buildings at this site in late 1974 (Murphy 1977).

Data collection.—Nests were inspected at 3–5-day intervals from 2 May–15 August 1977. Usually 4-day intervals were maintained, but if weather conditions were severe, the inspections were curtailed to avoid affecting nestling survival. Eggs were numbered and weighed to the nearest 0.1 g on a 5 g capacity Pesola scale and nestlings were weighed to the nearest 0.5 g on a 50 g capacity Pesola scale. Nestlings 5–6 days old were banded with a U.S. Fish and Wildlife Service aluminum band and also color leg bands after their weight reached 20 g. Nest height, tree height, tree basal diameter and distance between trees were measured directly with a tape measure. Tree volume was calculated assuming a conical shape for the trees [$V = {}^{1}/_{12}\pi$ (basal diameter)^2(height)]. Nest orientation was measured as the direction of a line from the center of the entrance to the back of the nest. Standard compass orientation was used; N = 0°, E = 90°, S = 180°, W = 270°.

Breeding success.—Estimates were sometimes needed to determine nestling age when first found, date of clutch initiation and 10-day nestling weight. The estimation procedures used were those of Murphy (1978a). As nests were not checked each day, it was not always possible to know the fate of some eggs and nestlings. Therefore, maximum and minimum estimates of success were used. The estimate of maximum hatching success was based on the assumption that eggs disappearing between successive nest checks hatched and the young subsequently died. The estimate of minimum hatching success was based on known hatch. The estimate of the minimum number of fledged nestlings was the number reaching a weight of 24.8 g or more (mean 10-day weight) before leaving the nest. The number of nestlings with a weight of 20.0 g before leaving the nest was the estimate of the maximum number fledged.

Data analysis.—Counts of the number of young fledged and eggs hatched were bimodally distributed due to a high frequency of nest failures. For this reason, the Mann-Whitney *U*-test was used for paired and the Kruskal-Wallis test was used for grouped comparisons of reproductive performance. Substantial variation existed in the reproductive output from the nests; both seasonal and per clutch output were investigated. Multiple regression analysis (BMDP2R, Dixon 1975) was used to determine the extent to which reproductive performance could be accounted for by variation in the continuous variables describing nest-site position. Where the data were normally distributed, *t*-tests were used for paired comparisons and correlation analysis used to investigate temporal variation.

RESULTS

The 2 spruce rows studied were oriented in a north-south direction on either side of the main ranch house. The average distance between the rows was 82 m. Both rows were bordered on 1 side by a honeysuckle hedge (*Lonicera* sp.). A plowed field, house, garage and driveway lay between the 2 rows (Fig. 1). Deciduous hedges and trees on the ranch were not used as nest-sites by the sparrows. The west tree row was more densely vegetated and more varied in tree size and number of nests per tree than the east tree row (Table 1). A significant positive regression was found when the frequency of nests was plotted against tree volume ($Y = 0.2014X + 0.0107$; $r = 0.562$, $P \leq 0.01$, $N = 60$). This was not a simple consequence of overpopulation as some box nests and former nest-sites in unoccupied trees remained vacant while large trees contained up to 14 nests. Almost all (97%, N = 146) nests were built adjoining the main trunk of a tree.

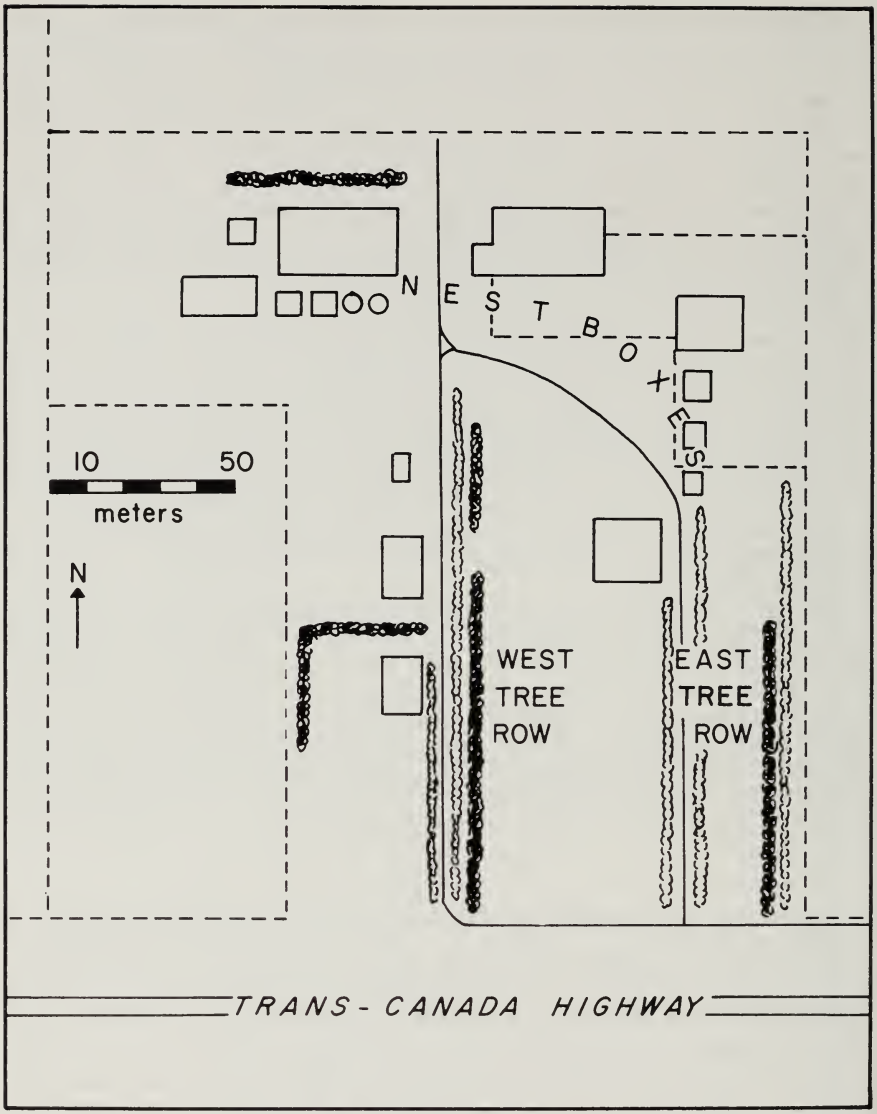


FIG. 1. Map of the study area. Major House Sparrow nesting occurred in rows of spruce windbreaks as well as in nest boxes attached to buildings on the ranch. Buildings are outlined, fence rows shown by dashed lines, roads by solid lines, hedgerows by irregular outlines and spruce rows by solid outlines. Only nests along the east tree row, west tree row and in the nest boxes provided the data for this study.

TABLE 1
SOME CHARACTERISTICS OF NEST-SITES IN THE EAST AND WEST ROWS

Variable	West row	East row	*U*-value
Total length (m)	94	81	NA
Total number of trees	34	24	NA
Total number of nests	110	36	NA
Mean tree height (m)	5.61**	4.50**	678
Mean inter-tree distance (m)	2.77**	3.58**	249
Mean tree volume (m^3)	13.42**	10.09**	692
Mean nest height (m)	3.87**	3.27**	1167
Mean distance to nearest neighbor (m)	0.66**	1.52**	439
Mean number of nests within 1 m	3.43**	0.76**	1345
Mean nest height/tree height ratio	0.69*	0.73*	610

* $P < 0.05$, Mann-Whitney *U*-test.
** $P < 0.01$ Mann-Whitney *U*-test.

Nest position.—Univariate inter-row comparison of means describing reproductive success show few differences (Table 2). No clear trends are apparent, but this is noteworthy since the average density of nests was much higher in the west row. Each row was then partitioned into 4 equal sections to determine whether position within a row affected reproductive performance. The west row displayed considerably more intra-row variation (Table 3). The nests were significantly more grouped in the southern half of the rows (west row: $t = 7.5$, df = 97, $P < 0.001$; east row: $t = 2.5$, df = 33, $P < 0.05$). In addition, the ratio of nest height to tree height increased from north to south along the west row.

TABLE 2
SEASONAL AVERAGES OF REPRODUCTIVE OUTPUT FROM BOX AND TREE NESTS

Variable	Box	West	East	H-stat.
Number of clutches[a]	2.71	2.12	2.06	8.86**
Total number of eggs	12.10	10.43	9.39	12.67**
Min. number hatching	7.50	5.43	4.89	12.24**
Max. number fledging	5.29	3.38	3.21	14.33**
Clutch-size	4.91	4.92	4.79	2.74
Min. hatch/clutch	2.86	2.70	2.57	1.86
Max. fledge/clutch	1.95	1.67	1.76	4.17
Egg weight	2.91	2.90	2.88	1.21
Nestling 10-day wt.	23.55	25.35	23.49	4.34

** $P < 0.01$ Kruskal-Wallis test.
[a] Lines connect groups not significantly different by comparison of rank sums (Dunn 1964).

Table 3

Average Values of Seasonal Reproductive Output for Nests along both Tree Rows; Each Row Was Partitioned into 4 Equal Sections: NQ = North Quarter, NM = North Middle, SM = South Middle, SQ = South Quarter

Variable	West tree row					East tree row				
	NQ	NM	SM	SQ	*H*	NQ	NM	SM	SQ	*H*
Sample size	27	18	14	30		6	8	8	7	
Nest height (m)	3.83	3.76	3.83	3.97	1.1	3.67	3.23	3.14	3.09	3.9
Nest height/tree height	0.62	0.68	0.70	0.74	12.2**	0.74	0.74	0.70	0.73	1.2
Nests within 1 m	2.67	2.44	4.50	4.20	6.4	0.28	0.55	1.11	0.92	3.84
Total clutches per nest	2.29	2.50	1.85	1.86	9.3*	2.28	2.00	2.00	2.00	3.09
Total eggs per nest	11.04	12.22	9.07	9.43	8.3*	9.71	9.22	9.33	9.37	1.14
Total fledging per nest	2.70	5.40	3.57	2.67	20.1**	2.12	3.66	4.00	2.12	1.97
Fledging success	0.56	0.78	0.67	0.62	3.2	0.49	0.74	0.78	0.66	1.84
Clutch-size	4.80	4.90	4.95	5.01	0.6	4.31	4.83	4.80	5.17	4.60
Fledging per clutch	1.35	2.35	1.88	1.54	8.2*	0.93	1.94	2.12	1.89	3.86

[1] Maximum value.
[2] Fledging success = number of fledglings/number of nestlings.
* $P < 0.05$.
** $P < 0.01$ (Kruskal-Wallis test).

Table 4 gives the average weather conditions prevailing in the Calgary region during the House Sparrow breeding season. The relatively strong northerly winds and high incidence of storms suggests that southerly position in a row or low nest height could enhance nest-site security. The earliest breeders suffered the most rigorous weather conditions of the breeding season, including 6 days of snow, 13 of rain and an average daily

Table 4

Climatic Table for Calgary, Alberta[a]

Month	Temperature (C)	Wind (m/sec)	Precipitation (mm)	No. of days of rain	Thunderstorms
April	3.6	SE 5.0	35	10	0.2
May	9.8	NW 5.0	52	11	1.4
June	13.0	N, NW 4.6	88	14	5.8
July	16.7	NW 4.1	58	11	8.2
August	15.1	N 4.0	59	12	5.3

[a] Data from R. A. Bryson and E. K. Hare (1974). Figures given represent multi-year means.

TABLE 5
SEASONAL VARIATION OF NEST ORIENTATION IN THE WEST ROW[a]

Portion of row		Nest orientation			
		NE	NW	SW	SE
Northern-most quarter	N =	5	7	8	8
		16 June	4 July	13 May	29 May
Middle half	N =	6	9	9	10
		9 June	14 June	16 May	11 May
Southern-most quarter	N =	5	8	10	8
		6 June	13 May	31 May	5 June
Whole row	N =	16	24	27	26
		4 June	10 June	17 May	21 May

[a] Dates are the average date of the initiation of first clutches for nests oriented in I of 4 directions: NE = 1°–90°, SE = 91°–180°, SW = 181°–270°, NW = 271°–360°.

minimum temperature of 3.5°C in May. Positive correlations between clutch initiation date and absolute and relative (to tree height) nest height indicated an early start for low nests. For means calculated over 10-day intervals, the correlation of clutch initiation date and absolute height was: $r = 0.809$, df = 9, $P < 0.01$, west row; and $r = 0.629$, df = 8, $P < 0.05$, east row; the correlation of clutch initiation date and relative nest height was $r = 0.630$, df = 9, $P < 0.05$, west row; and $r = 0.550$, df = 8, $P < 0.1$, east row.

Orientation.—Nests found in the spruce trees were bulky, ball-like structures composed of grasses, straw, small twigs and occasionally, paper, plastic and hair. The nest entrance was usually at the side of the structure, but it was frequently found on top or even underneath the main body of the nest. The direction in which the entrance faced was the measured orientation. When nests were grouped in 45° arcs, the nest entry directions were randomly distributed ($\chi^2 = 9.07$, df = 7, $P > 0.1$, NS). Nest entry direction depended on the date of first clutch initiation. North-facing nests (arc 270°–90°) were built by late nesters, particularly at the northern end of the west row (Table 5). The east tree row, perhaps due to restricted number of nest-sites showed little variation of nest orientation. Only 8 first clutches were initiated after 1 June along the east row; however, 5 of these were oriented either northeast or northwest. A trend for higher annual productivity from south-facing nests (arc 90°–270°) was noted. South-facing nests contained more successful clutches (2.26 vs 1.91) and correspondingly more fledglings (3.56 vs 3.11). In addition, the average number of fledglings per clutch was slightly higher for south-facing nests (1.74 vs 1.66).

TABLE 6

REGRESSIONS OF MEASURES OF REPRODUCTIVE SUCCESS ON NEST HEIGHT FOR BOTH ROWS AND THE WEST ROW ALONE[a]

Y	Both rows	West row alone
Total number of young fledging	$Y = -0.729X + 6.4$ $F = 6.1$, $P < 0.05$ df = 1, 106	$Y = -0.9575X + 6.6$ $F = 12.76$, $P < 0.01$ df = 1, 88
Total fledgling weight	$Y = -20.89X + 182.5$ $F = 6.52$, $P < 0.05$ df = 1, 106	$Y = -24.90X + 179.15$ $F = 10.19$, $P < 0.01$ df = 1, 88
Total nestling weight	$Y = -20.16X + 200.02$ $F = 6.4$, $P < 0.05$ df = 1, 106	$Y = -33.77X + 242.7$ $F = 11.21$, $P < 0.01$ df = 1, 88

[a] Residuals were checked for departures from normality (X = nest height in m).

Variation in productivity.—Significant relationships were found between measures of reproductive performance and simple parameters of nest-site position. Seasonal totals of number of young fledged, fledgling weight and nestling weight were negatively related to nest height (Table 6). There was a clear inverse relationship between the number and quality of fledged young and the height of the nests. This result is surprising because other factors known to influence House Sparrow breeding productivity, such as age and experience of the parents and the nutritional state of the female (Summers-Smith 1963, Dawson 1972, Pinowska 1979), did not mask the effect of nest height.

Many of the preceding analyses have assumed a relationship between nest-site exposure and security. Data from this study support this assumption. Eighteen nests were either destroyed or severely damaged after violent windstorms. All but 2 of the nests were oriented in a northerly direction and 61% (11 of 18) were in the northernmost quarter of each row. The ratio of nest height to tree height was slightly higher than average for the destroyed nests (west row: 0.72, east row: 0.77, see Table 1 for averages). All of the destroyed nests had at least one of the characteristics reducing nest-site security.

Box nests vs tree nests.—Seasonal totals of productivity were higher for birds nesting in boxes (Table 2). This probably occurred because more clutches were initiated at each box nest over the breeding season. First clutches were initiated earlier at box nests and the peak initiation of second clutches at box nests coincided with the peak of first clutch initiation at tree nests.

DISCUSSION

A unique aspect of this study site was the predominance of natural vs artificial nest-sites. The box nests were clearly the best nest-sites since clutches were initiated earlier in the box than tree nests. The observed increase in productivity at box nests is probably due to the protection afforded by the structure. They are impervious to wind damage, almost waterproof and probably provide a warmer micro-climate for the nest (Mertens 1977). The probability that an egg laid in a box nest resulted in a fledged young was 0.44; in contrast, for the tree nests, it was only 0.32 (west row) and 0.34 (east row). Differential productivity should also exist between differently positioned tree nests. The weather-related nest destruction supports the qualitative assessment that certain nest-sites and orientations are better suited to ambient conditions.

The attractiveness of large trees as nest-sites, the close proximity of the nests to the main trunks and the negative relationship between nest height and fledgling number all suggest the importance of nest-site security. Nests near the tops of spruce trees are exposed to rain and wind and wind-induced movements of the tree. Such movements may dislodge the nest more readily than the wind alone. The choice of spruce trees over deciduous trees for nest substrates is probably due to the thicker foliage and greater protection offered by the conifers.

Thunderstorms and strong winds are common in Calgary throughout the summer, but wind direction is predictable and a response to lower its effect would be anticipated (Austin 1974, Cink 1976). The decrease in the ratio of nest height to tree height towards the north end of both rows can be interpreted as a response to the usual wind direction.

The random distribution of nest entry direction is surprising considering the importance of nest orientation for other birds such as the Cactus Wren (*Campylorhynchus brunneicapillus*) and Verdin (*Auriparus flaviceps*) (Ricklefs and Hainsworth 1969, Austin 1974) and the demonstrated effect of weather on House Sparrow nests (Mitchell et al. 1973). Cactus Wrens orient their nest entrances into the wind to reduce heat stress on the nestlings. Kendeigh (1976) found that heat stress begins at 22°C in adult House Sparrows. Throughout July and August in Calgary, the maximum daily temperature often reaches or exceeds 22°C (23 days in 1977). This, combined with a long daylength and concomitant high level of incident radiation on the nests, could produce heat stress in nestlings. In Calgary, though, House Sparrows begin breeding in poor conditions relative to populations studied at lower latitudes (Murphy 1978a). Cool temperatures and rain early in the season combine to lower productivity compared to mid-summer values (Murphy 1978b, McGillivray 1978).

The preponderance of south-facing nests early in the season is perhaps a response to protect the nests from the north wind. The increase in the number of north-facing nests later in the season for both rows would be expected if wind ventilation were used as a cooling agent in warm weather. The change in average nest entrance orientation (Table 5) from early to late nesters may serve to minimize the detrimental influence of weather on reproductive output. The overall randomness of nest entry direction can be accounted for by the long House Sparrow breeding season and the resultant variation in optimal orientation.

The apparent relationship between average weather conditions and the pattern of nest position and construction may explain the variation in nest entrance orientation, nest height and the date of first clutch initiation. The better protected box nests allow birds to breed earlier, thus increasing the number of clutches possible in a season. Birds nesting in low tree nests begin to breed earlier and fledge more young. Birds nesting in south-facing nests begin to breed earlier and show marginally higher fledgling production. Sometimes the adaptive significance of the pattern is not entirely evident. Despite the presence of unused nest-sites, there is a strong relationship between the number of nests in a tree and tree size, suggesting that large trees make good nest substrates. Yet, there is no relationship between the number of fledglings from a nest and the size of the tree containing that nest.

These data imply that some of the variation in reproductive performance could be predicted with a knowledge of local climate and the position of the House Sparrow nests. However, as noted earlier, other variables affect reproductive output and may prevent the determination of the importance of weather. Recent banding recaptures at my study site have shown a large turn-over of birds. It is likely that at least 50% of the birds nesting on the ranch are either first-year birds or immigrants from neighboring ranches. Summers-Smith (1963) has shown that first-year birds start breeding later in the season and are less skilled at nest building than older adults. It is interesting that at this site the best protected nests were built by pairs who began to breed early. This suggests that the older adults built the early, and hence, more productive nests; unfortunately, the ages of the breeding birds were not known. Weather is clearly a major force determining the productivity of House Sparrows. Many nests on the study area were positioned to minimize the severity of the weather. The observation that many poor nest-sites were also chosen could be the result of experiments by first-year birds or simply an inability of pairs to find and maintain better sites.

SUMMARY

The variation in reproductive performance observed in this study appears to be partly attributable to the influence of weather. Box nests are well protected against the elements

and usually birds nesting in boxes were more successful than those nesting elsewhere. Tree nests are exposed and, to be productive, must be constructed to withstand strong winds, storms and cold temperatures. South-facing nests, central position along a tree row and low nest height to tree height ratio were determined to be beneficial in reducing the impact of the cool north winds. South-facing nests fledged more young early in the season, while north-facing nests were more productive in mid-summer. Throughout both tree rows, the number and weight of fledglings was negatively correlated with nest height.

ACKNOWLEDGMENTS

I express my gratitude to E. C. Murphy, whose own fieldwork and ideas prepared the groundwork for this study. Peter E. Lowther is given special thanks for preparing the figure and typing the manuscript. I am grateful to the Van family, the Jones family and Jerry de Zeeuw on whose lives I intruded for 4 months. H. Levenson, R. F. Johnston, J. T. Paul, Jr., A. M. Finfrock, J. A. Cox and P. W. Hedrick all read and commented constructively on the manuscript. Finally, I would like to thank my wife, Sandy, who aided immensely with fieldwork and tolerated protracted absences and an array of behaviors associated with the completion of this study. Support for this research was given by NSF grant BMS-76-02225 to R. F. Johnston.

LITERATURE CITED

Anderson, T. R. 1978. Population studies of European sparrows in North America. Occ. Paps. Mus. Nat. Hist., Univ. Kansas, No. 70.

Austin, G. T. 1974. Nesting success of the Cactus Wren in relation to nest orientation. Condor 76:216–217.

Bryson, R. A. and E. K. Hare. 1974. Climates of North America, Vol. 11 *in* World survey of climatology (H. E. Landsberg, ed.). Elsevier Scientific Publ. Co., Amsterdam, Netherlands.

Caccamise, D. F. 1977. Breeding success and nest-site characteristics of the Red-winged Blackbird. Wilson Bull. 89:396–403.

Cink, C. L. 1976. The influence of early learning on nest site selection in the House Sparrow. Condor 78:103–104.

Cody, M. L. 1971. Ecological aspects of reproduction. Pp. 461–512 *in* Avian biology, Vol. 1 (D. S. Farner and J. R. King, eds.). Academic Press, New York, New York.

Collias, N. E. 1964. The evolution of nests and nest-building in birds. Am. Zool. 4:175–190.

Dawson, D. G. 1972. The breeding ecology of House Sparrows. Ph.D. thesis, Edward Grey Inst., Oxford, England.

Dixon, W. J. (ed.) 1975. BMPD Biomedical Computer Programs. Univ. California Press, Berkeley, California.

Dunn, O. J. 1964. Multiple comparisons using rank sums. Technometrics 6:241–252.

Horn, H. S. 1968. The adaptive significance of colonial nesting in the Brewer's Blackbird *(Euphagus cyanocephalus)*. Ecology 49:682–694.

Inouye, D. W. 1976. Non-random orientation of entrance holes to woodpecker nests in aspen trees. Condor 78:101–102.

Kendeigh, S. C. 1976. Latitudinal trends in the metabolic adjustments of the House Sparrow. Ecology 57:509–519.

Lack, D. 1968. Ecological adaptations for breeding in birds. Methuen and Co., Ltd., London, England.

McGillivray, W. B. 1978. The effects of nest position on reproductive performance of the House Sparrow. M.A. thesis, Univ. Kansas, Lawrence, Kansas.

MERTENS, J. A. L. 1977. Thermal conditions for successful breeding in Great Tits *(Parus major* L.). II. Thermal properties of nests and nestboxes and their implications for the range of temperature tolerance of Great Tit broods. Oecologia 28:31–56.

MITCHELL, C. J., R. O. HAYES, P. HOLDEN AND T. B. HUGHES, JR. 1973. Nesting activity of the House Sparrow in Hale Co., Texas, during 1968. Ornithol. Monogr. 14:49–59.

MURPHY, E. C. 1977. Breeding ecology of House Sparrows. Ph.D. thesis, Univ. Kansas, Lawrence, Kansas.

———. 1978a. Breeding ecology of House Sparrows: spatial variation. Condor 80:180–193.

———. 1978b. Seasonal variation in reproductive output of House Sparrows: the determination of clutch size. Ecology 59:1189–1199.

ORIANS, G. H. 1961. Social stimulation within blackbird colonies. Condor 63:330–337.

PINOWSKA, B. 1979. The effect of energy and building resources of females on the production of House Sparrow *(Passer domesticus* (L.)) populations. Ekologia Polska 27:363–396.

RICKLEFS, R. E. AND F. R. HAINSWORTH. 1969. Temperature regulation in nestling Cactus Wrens: the nest environment. Condor 71:32–37.

ROBERTSON, R. J. 1973. Optimal niche space of the Red-winged Blackbird. Spatial and temporal patterns of nesting activity and success. Ecology 54:1084–1093.

SCHAEFFER, V. H. 1976. Geographic variation in the placement and structure of oriole nests. Condor 78:443–448.

SUMMERS-SMITH, D. 1963. The House Sparrow. Collins, London, England.

WILL, R. L. 1973. Breeding success, numbers and movements of House Sparrows at McLeansboro, Illinois. Ornithol. Monogr. 14:60–78.

MUSEUM OF NATURAL HISTORY, UNIV. KANSAS, LAWRENCE, KANSAS 66045.
ACCEPTED 30 SEPT. 1980.

WORKING GROUP ON GRANIVOROUS BIRDS—INTECOL

The Third International Congress of Ecology will take place in Warsaw, Poland, 5–11 September 1982. The Working Group on Granivorous Birds—INTECOL—is organizing a special symposium along the theme of "The role of granivorous birds, especially Corvidae and Columbidae, in ecosystems." Such problems as population dynamics, biomass and production rates, energetics, impact of granivorous birds on ecosystems and management of pest situations will be covered.

All correspondence and requests for scientific information should be sent to: Prof. Dr. Jan Pinowski, Institute of Ecology PAN, Dziekanow Lesny, 05–150 Łomianki, Poland or by telex 817378 IEPANPL.

Wilson Bull., 93(2), 1981, pp. 207–217

CANADA GOOSE BROOD BEHAVIOR AND SURVIVAL ESTIMATES AT CREX MEADOWS, WISCONSIN

Michael C. Zicus

Many studies have reported on the biology of Canada Goose (*Branta canadensis*) broods in a variety of geographical locations and habitat types. Different methods based on observations of both marked and unmarked broods, however, have yielded a wide range of results concerning brood loss, brood mixing and gosling survival. This paper reports on a study of Canada Goose broods in a managed, reestablished flock. The objectives were to describe certain aspects of the behavior and survival in individually identified broods, to examine some potential biases inherent in goose brood studies and to compare the results with data collected in other studies.

STUDY AREA AND METHODS

The study was done at the 12,185-ha Crex Meadows Wildlife Management Area in northwestern Wisconsin near Grantsburg, Burnett Co. The Wisconsin Department of Natural Resources began management of marsh-prairie habitats on Crex Meadows in 1947 and an effort to reestablish nesting Giant Canada Geese (*B. c. maxima*) began in 1952 (Hunt and Jahn 1966). Production of goslings increased from virtually nothing in 1957 to approximately 480 in 1973 (Zicus 1974:83). These Canada Geese are migratory and usually arrive in early March and begin nesting in mid-March or early April. Nesting now occurs throughout the study area, but most brood rearing takes place in 5 marshes. Accordingly, other marshes are used very little by Canada Geese during the summer.

Wetlands vary in size from less than a hectare to several hundred hectares in size. Many wetlands are shallow sedge (mostly *Carex stricta*) and grass (mostly *Calamagrostis canadensis*) meadows. There are also numerous impounded marshes with varying amounts of open water, emergent vegetation and floating mats of sedge (*Carex* spp.) and cattail (*Typha angustifolia*). Uplands are forests of jack pine (*Pinus banksiana*) and northern pin oak (*Quercus ellipsoidalis*) and brush-prairie savanna (Vogl 1964). The area has had a long fire history, and habitats are managed intensively through controlled burning of wetlands and uplands and the manipulating of water levels in many once drained marshes. Approximately 121 ha of cropland are also planted annually in the center of the management area to provide supplemental food for wildlife.

Sixty-three marked families from known nest locations and 74 marked pairs with goslings from undiscovered nests were observed. Several marking techniques were used, but most of the data involved 131 families in which one or both of the adults had vinylite neckbands (Sherwood 1966a). Limited data were also obtained from 6 clutches of eggs injected with vegetable dyes (Evans 1951). Geese were captured by cannon netting in autumn (Dill and Thornsberry 1950), summer drive trapping (Cooch 1955) and mist netting nesting females (Zicus 1975). Nests were located in 1972–1974 by intensively searching the study area on foot and from a canoe. Clutch-size, fate of the clutch, egg fertility and number of goslings hatched were determined for each nest.

Observations were made daily from dike roads and accessible points in the marshes. Time of day, number of broods seen together, number of goslings in each family, gosling age, as

well as location and activity were recorded for all marked families observed. The ages of goslings hatched from undiscovered nests were estimated by comparing gosling size, plumage and behavior with goslings in known-age broods. Goslings, usually brooded on the nest until the morning after hatching (Cooper 1978:53), were considered 1 day old at departure. All references to broods are to individually identified broods unless otherwise stated.

Gosling survival was estimated at 7-day intervals each year by counting goslings with neckbanded adults. Survival during the first 7 days after hatching was determined using the last complete gosling count during the first week after hatching for marked families whose numbers at hatching were known. Estimates for each week of age up to 8 weeks were made using the last gosling counts from families observed in consecutive weeks. Weekly survival estimates determined in this way should not have been biased by gosling adoption if the marked pairs under observation adopted goslings and lost goslings to adoption at the same rate as those pairs not being observed during the 7-day interval.

The survival of goslings through 8 weeks of age was estimated by 2 methods. The first method combined weekly survival estimates, while the second involved a modeling process using a number of reproductive parameters estimated during the study. These estimates included the proportion of the pairs raising broods through 8 weeks (successful pairs) and the proportion of the pairs hatching goslings but not raising a brood (unsuccessful pairs), and the average brood size at hatching for both successful and unsuccessful pairs. This allowed the number of goslings hatched by any given number of pairs to be determined. Next the number of goslings hatched by both successful and unsuccessful pairs was multiplied by the apparent gosling survival for each type of pair. The apparent survival of goslings in broods of unsuccessful pairs was zero, while the apparent survival in broods with successful pairs was determined by comparing the numbers of 8-week-old goslings with different marked pairs to the number of goslings hatched by these pairs. In this way, the total number of goslings alive after 8 weeks could be compared with the total number hatched by any given number of pairs.

RESULTS

Canada Geese were never observed rearing broods singly on marshes that were not being used by other families. Many Canada Goose pairs left their nesting marshes soon after hatching a brood (Table 1). Between 60 and 67% of all marked families moved, although, in many cases, the nesting marshes appeared to be similar to those used for brood rearing. Furthermore, 25–53% of the pairs observed nesting successfully on a major brood rearing marsh also moved their young to a different brood rearing marsh.

The time between departure from the nest and the first observation of a brood on the marshes used for brood rearing was short and suggested immediate and direct movement to the brood rearing marshes (Table 2). One family was observed 4.8 km from the nest within 24 h of leaving the nest; in 2 consecutive years, another pair moved their broods 8.4 km in a maximum of 2 days. Almost 53% of the families originating from nests in major brood rearing marshes were observed on a different marsh within 4 days after departure from the nest. Similarly, 40% of the broods leaving nests in marshes that were not used for brood rearing were observed on another marsh within 4 days.

TABLE 1
EARLY MOVEMENT OF MARKED CANADA GOOSE FAMILIES, 1972–1974

Marked families	1972	1973	1974	All years
All successful nests	9	20	22	51
Broods leaving marsh	6	12	14	32
Percent	67	60	64	63
Successful nests in major brood rearing marshes	4	15	17	36
Broods leaving marsh	1	7	9	17
Percent	25	47	53	47

Distances between the nest locations and the centers of the marshes that were first used for brood rearing ranged from 0.7–8.4 km (Table 3). The major brood rearing marshes were centrally located and Canada Goose families leaving nests in these marshes did not have to move as far to reach other major brood rearing marshes as families from nests in peripheral marshes. Nonetheless, 41% of the families from nests in major brood marshes moved more than 3.0 km to reach their initial brood marshes. The longest distances moved were those from nesting marshes that were not used for brood rearing with 27% of these families moving more than 7.5 km.

Canada Geese usually remained on their first brood rearing marsh for the entire brood rearing period. For the 3 years, an average of 86% (N = 70) of the marked pairs were observed each year on only 1 brood rearing marsh. In contrast, 10 pairs (14%) were seen during the early portion of the brood rearing period on 1 marsh and later on a second marsh. The

TABLE 2
NUMBER OF DAYS BETWEEN NEST DEPARTURE AND FIRST OBSERVATION OF CANADA GOOSE BROODS ON MARSHES OTHER THAN THE NESTING MARSHES, ALL YEARS COMBINED

Days since leaving nest	Hatched in major brood rearing marshes		Not hatched in major brood rearing marshes		All broods	
	N	%	N	%	N	%
1–4	9	53	6	40	15	47
5–8	1	6	4	27	5	16
9–12	2	12	1	7	3	9
13–16	1	6	1	7	2	6
17–20	1	6	0	0	1	3
21+	3	18	3	20	6	19

TABLE 3

DISTANCES BETWEEN NEST LOCATIONS AND CENTER OF INITIAL BROOD REARING MARSHES USED BY CANADA GOOSE BROODS LEAVING NESTING MARSHES, ALL YEARS COMBINED

Distance (km)	Hatched in major brood rearing marshes		Not hatched in major brood rearing marshes		All broods	
	N	%	N	%	N	%
0.0–1.5	4	24	2	13	6	19
1.6–3.0	6	35	8	53	14	44
3.1–4.5	5	29	1	7	6	19
4.6–6.0	2	12	0	0	2	6
6.1–7.5	0	0	0	0	0	0
7.6–9.0	0	0	4	27	4	12

movement to a second marsh usually occurred within a few days of the time the adults molted their flight feathers. Movement distances between the center of the initial and second brood rearing marsh ranged from 1.4–4.8 km and averaged 2.3 km.

The brood rearing period was divided into pre-molt and post-molt segments to examine yearly fidelity to specific brood rearing marshes. Individual pairs were faithful to specific marshes from year to year. Before molting, 11 pairs successfully raising broods in 2 consecutive years and 2 pairs raising broods in 3 consecutive years used the same marshes each year. Likewise, after molting and before gaining flight, 13 pairs raising broods in 2 consecutive years and 2 pairs raising broods in 3 consecutive years used the same marshes. In addition, 2 pairs moving to a second marsh for the post-molt segment during the same season made a similar move when rearing young in a second year. Another pair used the same marsh through the brood period in 1972 and 1973, but used a different marsh through the brood period in 1974.

Of 3 marked females with previous brood rearing experience that paired with different ganders and 5 marked males with previous experience rearing broods and paired with different females, all 3 females used the same marshes they last used, while 2 of the 5 ganders reared broods on marshes other than the one they last used. In 1 case, both members of the new pair had previously raised broods on different marshes. The goslings hatched by this pair were raised on the marsh last used by the female and not the male.

As broods began to concentrate in the brood rearing areas, both marked and unmarked broods fed together along dikes and on floating mats of vegetation. At times, goslings became separated from their parents and

TABLE 4

MINIMUM ESTIMATES OF GOSLING ADOPTION FOR CANADA GOOSE PAIRS BY WEEKLY BROOD-AGE INTERVALS, ALL YEARS COMBINED

Brood-age interval	Pairs observed	Pairs showing increased brood size	
		N	%
Hatch–week 1	46	11	24
Week 1–week 2	42	11	26
Week 2–week 3	47	7	15
Week 3–week 4	49	8	16
Week 4–week 5	40	4	10
Week 5–week 6	27	2	7
Week 6–week 7	26	2	8
Week 7–week 8	23	1	4

broodmates, and many were adopted into other families; of 87 pairs observed during the 3 years, a minimum of 40 (46%) adopted goslings at some time. All pairs adopting goslings could not be determined, because all broods were not observed frequently enough to detect gosling adoption that compensated for goslings lost to other pairs or through mortality. However, based on observations of only those broods increasing in size, a minimum of 36–50% of the marked pairs adopted young into their broods between hatch and 8 weeks of age. Adopted goslings were usually about the same age as their new broodmates.

Adoption was most common during the first 2 weeks after hatching (Table 4). The number of goslings associated with some pairs would change daily as the broods fed on mats of vegetation or moved from favored feeding sites along the dikes. Sometimes, goslings joining another brood would rejoin their own family within several minutes. Other instances of adoption appeared to be more permanent, and limited gosling adoption continued through 8 weeks of age.

An average of 24.2% of the successful nesting pairs did not raise broods to flight (range 17.9–33.3%). Pairs raising broods and those that did not had different reproductive characteristics (Table 5). Egg fertility, egg success and the average brood size at hatching were significantly lower for pairs that did not raise a brood ($\chi^2 = 8.21$, df = 1, $P < 0.01$; $\chi^2 = 6.74$, df = 1, $P < 0.01$; and $t = 2.24$, df = 60, $P < 0.05$). Pairs that did not raise young also tended to have lower average clutch-sizes ($t = 1.19$, df = 60, $P = 0.24$ [NS]), but not different hatching success ($\chi^2 = 0.02$, df = 1, NS). In addition, a greater proportion of the pairs that failed to raise young also tended to have at least one 2-year-old pair member than did those pairs that successfully raised young.

Table 5

Brood Rearing Success and Reproductive Characteristics of Successful Nesting Canada Geese, 1972–1974

Characteristic	Raised brood (N = 47)	Did not raise brood (N = 15)
Average clutch	5.8	5.3
Fertility (%)	92.7	81.1
Hatching success (%)[a]	97.4	95.0
Egg success (%)[b]	86.2	73.6
Average brood size at hatching[c]	5.0	3.9

[a] Equals percent of fertile eggs that hatch (Cooper 1978:61).
[b] Equals percent of all eggs that hatch (Cooper 1978:61).
[c] Equals average clutch times egg success.

Most gosling mortality occurred during the first 12 days after hatch (Table 6). In 1 interval, a survival estimate greater than 100% was obtained when the observed pairs adopted more goslings than they lost to adoption in the interval. Based on the combination of weekly estimates, gosling survival through 8 weeks averaged 61.2% (range 47.7–71.5%) during the study. By comparison, the apparent survival to 8 weeks in broods with successful pairs averaged 80.5% (range 76.7–82.9%), but estimated gosling survival was lowered to an average of 62.5% (range 60.7–70.5%) when the reproductive performance of the flock was modeled to include goslings produced by pairs unsuccessful in rearing a brood. Both estimates based on a combination of weekly survival rates and those based on modeling reproductive performances gave similar results in each year.

Table 6

Canada Goose Gosling Survival Estimates by Weekly Age Intervals, 1972–1974

Brood-age	Average age (days)	No. of broods	Survival (%)
Hatch–week 1	5	30	86.5
Week 1–week 2	12	32	76.9
Week 2–week 3	20	28	98.5
Week 3–week 4	26	33	100.0
Week 4–week 5	33	31	100.8
Week 5–week 6	40	21	96.7
Week 6–week 7	46	15	97.3
Week 7–week 8	56+	15	98.5

DISCUSSION

The movement of Canada Goose broods from nest locations to brood rearing areas immediately after hatching at Crex Meadows was similar to that reported for Canada Geese in other areas. Canada Goose brood movements to selected rearing marshes depend, in part, on the distribution of rearing habitat in relation to nesting areas. Geis (1956:416) reported that geese nesting on islands where no food was available in Flathead Lake, Montana, moved broods to rearing areas 6–10 miles (10–16 km) away immediately after hatching; those geese nesting along the Flathead River moved broods downstream from the nest-sites to brood rearing areas. MacInnes and Lieff (1968:99–101) observed that broods near the McConnell River in the Northwest Territories moved 10–15 km from nest locations to feeding areas. In contrast, Dimmick (1968:53) reported goose broods at Jackson Hole, Wyoming, left the immediate vicinity of the nest, but remained in the nesting area for several weeks. Most individual pairs and females at Crex Meadows made the same movements to a brood rearing area each year, and once there, they rarely changed location until the young were grown and the adults had regained flight. Similarly, Geis (1956:416) reported that broods rarely moved to other rearing grounds once they were established on a rearing area, and Martin (1964:23) observed many pairs at Ogden Bay, Utah, using the same rearing areas in consecutive years.

The patterns of rearing marsh selection observed at Crex Meadows have probably developed with the growth of the flock and reflect the distribution of marshes with food and molting security and the preference of individual nesting females. Cooper (1978:23) reported individual female Canada Geese nesting in approximately the same locations each year, and Martin (1964:16) and Brakhage (1965:768) observed older geese establishing nests first. These factors may force novice nesters to establish territories in the available unoccupied habitat which may or may not be near the brood rearing marshes. Sherwood (1966b:70) reported novice nesting 2-year olds nested and/or raised their broods in the same general area that they had been hatched or reared in, but did not discuss any specific influence on site selection by the male or the female of the pair. Martin (1964:23), however, was unable to observe any definite pattern in rearing area selection by adults with their young in Utah. The movements of broods to rearing areas and from rearing marshes used for nesting to different ones that were observed at Crex Meadows could persist if geese established nests wherever possible in the marshes, but females preferred the marshes for brood rearing that they had previsouly used. I speculate that females may initially use the marshes that they themselves were raised in, thus explaining how these movement patterns might evolve. Numerous authors

have concluded that the female Canada Goose rather than the male chooses the nest-site (Collias and Jahn 1959:485, Brakhage 1965:757, and others), and that rearing marsh selection may be similar and may depend on the initial and subsequent experiences of the female.

Crex Meadows goslings were commonly adopted from one brood to another. Gosling adoption was most prevalent during the first 2 weeks of age, but occurred until at least 8 weeks of age. In contrast, Martin (1964:25) observed no change in brood size after 3 weeks of age, and Sherwood (1966b:124–127) found that brood size changes were most prevalent during the first 2 or 3 weeks, but that they still occurred into the fourth week after hatch. Sherwood (1966b:129) also reported that goslings could not recognize their broodmates or parents until 5 or 6 weeks of age. Unlike observations in Missouri (Brakhage 1965:767), abnormally large broods or broods escorted by more than 1 pair formed infrequently and were never observed with marked pairs at Crex Meadows.

The loss of entire broods at Crex Meadows was similar to that reported at the Seney National Wildlife Refuge (NWR), but different from that reported near the McConnell River. At least 6 of 20 marked pairs observed at the Seney NWR in 1965 lost their entire broods (Sherwood 1966b:132); brood loss may have been even greater if some pairs lost their broods before Sherwood first observed them. However, only 3 of 96 marked pairs lost entire broods near the McConnell River (MacInnes et al. 1974:696). Pairs losing broods at Crex Meadows had smaller clutches with lower fertility and hatched fewer young; these characteristics have been associated with younger birds (Brakhage 1965:760, Cooper 1978:53, 74). Sherwood (1966b:130–131) also observed 4 of 6 marked pairs with 2-year-old females lose their broods. While not defining the phrase, he concluded that the ability to hold a brood was related primarily to the "age of the pair." Since he presented only data on the ages of the females in the marked pairs, I believe he was referring primarily to female age when discussing "age of the pair." Other aspects of pair age, such as the age of the gander or the length of time individual geese had been mated, could also be important if older geese and those mated for the longest time developed the strongest brood rearing abilities. Sherwood (1966b) further concluded that the ability to hold a brood was secondarily related to the size of the brood at hatching. The actual size of the brood might be important if goslings, unable to recognize their parents or broodmates, were attracted to larger broods as Sherwood speculated. Broods were concentrated at both Crex Meadows and the Seney NWR, where brood loss was higher, whereas they were more dispersed at the McConnell River where loss was lower. The greater loss of broods at Crex Meadows and the Seney NWR probably resulted from prolonged contacts between different pairs

with those pairs made up of the youngest geese, or perhaps those paired for the shortest time the most likely to lose golsings.

Studies relying solely on marked geese to estimate gosling survival are few in number and make comparisons with Crex Meadows difficult. MacInnes et al. (1974:697–699) reported that the survival of goslings with neckbanded adults, from 6 days before hatching to approximately 7 days of age, ranged from 64.7–87.3% near the McConnell River. Survival from 7–35 days of age was 91.9–99.3%. When the McConnell River estimates are combined with the approximate 3% loss of entire broods MacInnes et al. (1974:697) reported, survival to 35 days old ranged from 60.0–83.7% with a 5-year mean of 72.6%. In comparison, survival to 33 days old at Crex Meadows ranged from 57.2–81.0% with a 3-year mean of 64.7%.

Gosling survival has been determined in other studies by comparing total goslings hatched with the goslings alive at some time later or by observing changes in average brood size over a period of time. Estimates using total gosling counts are as reliable as the investigator is accurate in determining the number of goslings hatched that use a specific rearing area and in subsequently counting all survivors from this group of goslings. In many situations, accurate counts of all goslings hatched in an area are almost impossible. Estimates obtained using total gosling counts have ranged from 80–84% in Montana (Geis 1956:417), 64–80% in Missouri (Brakhage 1965:768) and 16–78% in Michigan (Sherwood 1966b:47). In comparison, survival estimates based on average brood size comparisons are biased if any pairs lose their entire brood. Estimates using this method have sometimes revealed average brood sizes greater than the average hatch per successful nest (Williams and Marshall 1938:17–18, Steel et al. 1957:4, Martin 1964:50). These authors estimated gosling survival until late in the brood period at 93–97%.

The behavior of Canada Goose broods at Crex Meadows created a serious potential bias for estimating gosling survival and flock production. More than half of the marked pairs observed with broods were from nests that were not found. This resulted from my inability to find all the nests on Crex Meadows and the tendency for geese to move broods considerable distances to brood rearing marshes. As a result, gosling survival could not be assessed by comparing total goslings hatched with total goslings alive at some time later. Likewise some successful nesting pairs lost all of their goslings to mortality and/or to adoption into other broods. If gosling survival was calculated by a comparison of average brood size at hatching to the average brood size at fledging, production would have been overestimated by an average of 27%. These potential biases seem likely to exist to varying degrees in any goose brood study. The degree to which esti-

mates will be biased depends on the behavior of pairs and their young. Consequently, gosling survival and production estimates without the benefit of marked geese should be viewed cautiously.

SUMMARY

A study of marked Canada Geese examined the use of brood rearing areas and brood and gosling survival between 1972 and 1974 in managed marshes in northwestern Wisconsin. Between 60 and 67% of the pairs hatching goslings moved them to 1 of 5 major rearing marshes where there were other broods. However, 25–53% of the pairs nesting on a major brood rearing marsh also moved to a different brood rearing marsh to raise their young. Movements of all pairs with broods ranged from 0.7–8.4 km, and were made immediately after hatch with 47% of the families reaching their first rearing marsh in less than 4 days. Once on a rearing marsh, families rarely moved to another. Almost all pairs raised young on the same marshes in subsequent years. Observations of males and females with previous brood rearing experience that had formed new pairs between years suggested females may influence the selection of a brood marsh. At least 36–50% of the pairs adopted goslings into their broods at sometime between hatch and 8 weeks. Adoption was most prevalent before goslings were 2 weeks old. From 18–33% of all pairs failed to raise their young to flight. These pairs also had lower egg fertility and brood sizes at hatching than pairs raising young. Overall gosling survival determined by the observation of young in marked broods ranged from 60.7–70.5%. Serious biases due primarily to the behavior of the broods affected survival estimates determined in other ways with production being overestimated by an average of 27% if the loss of entire broods was not considered.

ACKNOWLEDGMENTS

Special thanks to W. H. Marshall for his suggestions during the study and for reviewing the manuscript. N. R. Stone and J. O. Evrard, of the Wisconsin Department of Natural Resources, and the other members of the Crex Meadows staff provided valuable assistance in the field, while R. A. Hunt provided helpful comments on the study and with J. Bartelt reviewed the manuscript. University of Minnesota graduate students and A. H. Grewe with students from St. Cloud State University, St. Cloud, Minnesota, helped capture the many geese banded in this study while J. A. Cooper contributed in many ways. Financial support was provided by a National Defense Education Assistantship, the Malvin E. and Josephine D. Herz Foundation, the Dayton's Natural History Fund and the Department of Entomology, Fisheries and Wildlife at the University of Minnesota. This is Paper No. 11660 of the Scientific Journal Series of the Minnesota Agricultural Experiment Station.

LITERATURE CITED

Brakhage, G. K. 1965. Biology and behavior of tub-nesting Canada Geese. J. Wildl. Manage. 29:751–771.

Collias, N. E. and L. R. Jahn. 1959. Social behavior and breeding success in Canada Geese (*Branata canadensis*) confined under semi-natural conditions. Auk 76:478–509.

Cooch, G. 1955. Modifications in mass goose trapping technique. J. Wildl. Manage. 19:315–316.

Cooper, J. A. 1978. The history and breeding biology of Canada Geese of Marshey Point, Manitoba. Wildl. Monogr. 61.

Dill, H. H. and W. H. Thornsberry. 1950. A cannon projected net trap for capturing waterfowl. J. Wildl. Manage. 14:132–137.

Dimmick, R. W. 1968. Canada Geese of Jackson Hole, their ecology and management. Wyoming Game Fish Comm. Bull. No. 11.

Evans, C. D. 1951. A method of color marking young waterfowl. J. Wildl. Manage. 15:101–103.

Geis, M. B. 1956. Productivity of Canada Geese in the Flathead Valley, Montana. J. Wildl. Manage. 20:409–420.

Hunt, R. A. and L. R. Jahn. 1966. Canada Goose breeding populations in Wisconsin. Wisconsin Conserv. Dept. Tech. Bull. 38.

MacInnes, C. D. and B. C. Lieff. 1968. Individual behavior and composition of a local population of Canada Geese. Pp. 93–101 *in* Canada Goose management (R. L. Hine and C. Shoenfeld, eds.). Dembar Educational Res. Serv. Inc.

———, R. A. Davis, R. N. Jones, B. C. Lieff and A. J. Pakulak. 1974. Reproductive efficiency of McConnell River small Canada Geese. J. Wildl. Manage. 38:686–707.

Martin, F. W. 1964. Behavior and survival of Canada Geese in Utah. Utah State Dept. Fish Game Infor. Bull. 64–67.

Sherwood, G. A. 1966a. Flexible plastic collars compared to nasal discs for marking geese. J. Wildl. Manage. 30:853–855.

———. 1966b. Canada Geese of the Seney National Wildlife Refuge. Ph.D. thesis, Utah State Univ., Logan, Utah.

Steel, P. E., P. D. Dalke and E. G. Bizeau. 1957. Canada Goose production at Gray's Lake, Idaho, 1949–51. J. Wildl. Manage. 21:38–41.

Vogl, R. J. 1964. Vegetational history of Crex Meadows, a prairie savanna in northwestern Wisconsin. Am. Midl. Nat. 72:157–175.

Williams, C. S. and W. H. Marshall. 1938. Survival of Canada Goose goslings, Bear River Refuge, Utah, 1937. J. Wildl. Manage. 2:17–19.

Zicus, M. C. 1974. A study of the giant Canada Geese nesting at Crex Meadows, Wisconsin. M.S. thesis, Univ. Minnesota, St. Paul, Minnesota.

———. 1975. Capturing nesting Canada Geese with mist nets. Bird-Banding 46:168.

DEPT. ENTOMOLOGY, FISHERIES, AND WILDLIFE, UNIV. MINNESOTA, ST. PAUL, MINNESOTA 55108. (PRESENT ADDRESS: MINNESOTA DEPT. NATURAL RESOURCES, WETLAND WILDLIFE RESEARCH GROUP, BEMIDJI, MINNESOTA 56601.) ACCEPTED 2 JUNE 1980.

Wilson Bull., 93(2), 1981, pp. 218–242

BREEDING BIRD POPULATIONS IN THE GREAT SMOKY MOUNTAINS, TENNESSEE AND NORTH CAROLINA

S. Charles Kendeigh and Ben J. Fawver

The analysis of bird populations in mountain systems, such as the Great Smoky Mountains, is of special interest because of the relations of these populations to the mosaic of vegetation types and to variations in climate and physical conditions that occur. The Great Smoky Mountains of eastern Tennessee and western North Carolina lie at the southern end of the Appalachian Mountain System, escaped glaciation during the Pleistocene epoch, have sufficient elevation to provide a considerable gradient of temperature and contain a variety of slope exposures with striking contrasts in moisture conditions (Shanks 1954, Whittaker 1956).

The many different types of vegetation in the Great Smoky Mountains National Park are in nearly virgin condition. The deciduous plant communities have remained relatively undisturbed since the early Tertiary, and their diversity of plant species is the richest within the deciduous forest biome. Coniferous forests of different types and past history occur at both low and high elevations.

Breeding bird censuses were taken in 26 areas, representing 8 types of climax or relatively stable vegetation and 4 seral stages. The fieldwork was carried out during June and July 1947 and from May through July 1948.

PLANT COMMUNITIES

The vegetation shows a continuum of change with elevation and slope exposures (Fig. 1). For convenience, however, separate plant communities are recognized, based on their dominant species (Whittaker 1956).

Cove hardwoods occur characteristically at lower elevations in moist shaded coves and on north-facing slopes. Eastern hemlock (*Tsuga canadensis*) occurs in some cove forests in mixed or nearly pure stands. Chestnut oak (*Quercus prinus*) (chestnut) and oak-hickory forests prevail on east and west slopes, while on exposed, drier south and southwest slopes, subject also to more frequent fires, southern pine (*Pinus* spp.) forest or pines with an undergrowth of heath predominate.

At intermediate elevations, cove forests extend up into beech forests in gaps between mountains or on sheltered slopes, northern red oak (*Q. rubra*) (chestnut) and white oak (*Q. alba*) (chestnut) forests replace the chestnut oak (chestnut) forest, while on exposed ridges grassy balds replace trees. Chestnut (*Castanea*) is, of course, no longer a dominant, although at the time of this study many dead stubs scattered through the forest indicated their former importance. At cooler high elevations, spruce (*Picea*)-fir (*Abies*) forests predominate, although they give way to heath balds on xeric exposed ridges.

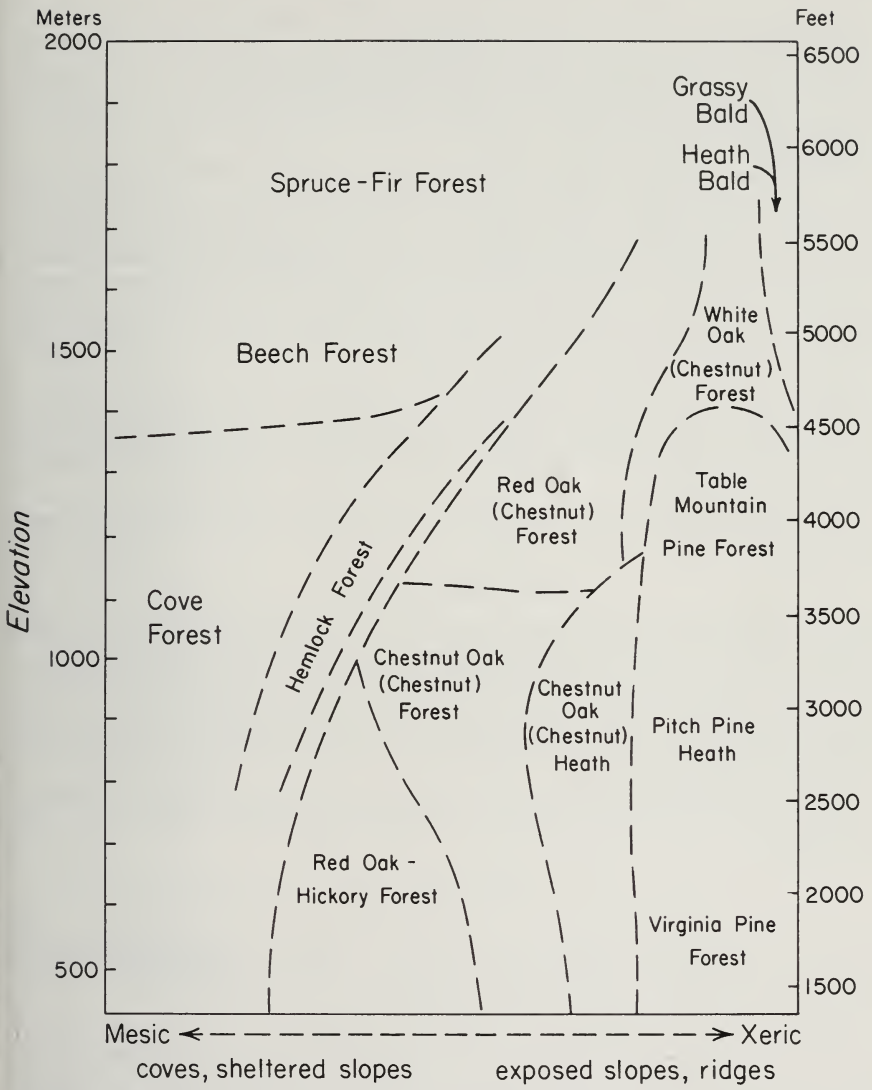


FIG. 1. Mosaic of plant communities showing variations with elevation and slope exposure (modified from Whittaker 1956).

METHODS OF ANALYSIS

Bird populations.—The spot-map method for censusing breeding birds was used where the terrain and available time permitted. Areas varied in size and shape depending on terrain and slope. They ranged from 6–12 ha (Table 1), which are rather small areas, but since each major vegetation type was censused at different localities, the total area covered in each

vegetation type was at least 23 ha and usually over 40 ha. Boundaries were measured with a steel tape or by pacing and mapped to scale. Use was made of natural landmarks and of numbered white cards nailed to trees at 50-m intervals for locating birds, especially singing males, on maps. In several instances, areas were long strips along trails and only 1 line of markers was used. Bird counts were obtained in each area at least 4 times in 1947 and 5 times in 1948.

Cruising counts only were taken of singing males in several areas. These areas were of known size and thoroughly covered on each count. Two to 6 counts were made on each area; the largest number of each species observed on any count was taken as the population of that species. This follows Palmgren's (1930) procedure except that no corrections were made for smaller values often obtained with fewer than 4 or 5 counts. Ten comparable censuses obtained by spot-map and cruising procedures in 5 different types of vegetation, although not in the same area the same year, showed only a slight tendency for population size estimates to be lower with the cruising procedure.

Species occurring in different plots of the same vegetation type have been combined and their population sizes averaged (Table 2). Persons wishing the precise location, more complete description of the vegetation and data on the bird population of each sample plot should consult the doctorate thesis of the junior author (Fawver 1950) filed in the University of Illinois Library, Urbana.

Data.—Coefficients of species similarity (S_s) were calculated with the Sørenson equation (Able and Noon 1976):

$$S_s = 2C/(A + B)\cdot 100$$

where C represented number of species common to the 2 communities and A and B total number of species in each community. Multiplying by 100 transfers coefficients into percentages. In these comparisons, species were included with less than 0.5 pairs/40 ha (shown by + marks in Table 2). Larger-sized sampling areas would doubtless have permitted quantification of their densities. Percentages higher than 50 indicate that the 2 communities have more species alike than different.

The above equation does not evaluate the difference in abundance (number of pairs) of a species when it occurs in both communities. Coefficients of population similarity (S_p) were obtained by:

$$S_p = 1.0 - \frac{\Sigma(p_a - p_b)}{P_a + P_b}$$

where p_a is the population of a species in community a and p_b in community b and P_a and P_b are total populations of all species in communities a and b, respectively (Odum 1950). In this calculation the plus sign in Table 2 was taken as zero population.

The Shannon-Weiner species diversity index ($H' = \Sigma p \log_e p$) and equitability index ($J' = H'/H'_{max}$) were calculated for the birds in each plant community where p is the proportion each species population is of the whole and H'_{max}, the maximum possible diversity for the given population size and number of species, is the logarithm of the number of species (Pielou 1966, Sheldon 1969).

Mean number of pairs per species (p/s) and median population of each species were also determined. Skewness (g_1) in the distribution of population sizes among species in a community was calculated with the equation (Zar 1974):

$$g_1 = \frac{(x - \bar{x})^3}{(n - 1)(n - 2)(sd)^3/n}$$

where $x_1 = p/s$ for a species, $\bar{x}$ is the mean p/s, n is number of species, and sd is standard deviation. Testing for statistical significance was performed using Table D25 of Zar (1974).

Table 1

Census Areas and Bird Censusing Methods

Plant community and location	Size (ha)	Spot-mapping		Cruising counts	
		1947	1948	1947	1948
Pine-oak forest					
Mature, 6.4 km NW of Gatlinburg	12.0	√	√		
Seral, opposite Park Headquarters	10.2	√	√		
Seral, 1.6 km farther south	6.0		√		
Cove forest					
Porters Creek	7.2		√		
Porters Creek	9.2			5	
Ramsey Prong	12.8				5
Ramsey Prong	6.8	√			3
Ramsey Prong	6.0		√		
Hemlock-deciduous forest					
Roaring Fork	10.0		√		
Roaring Fork	8.0				2
Brushy Mountain	11.6	√			4
Chestnut oak (chestnut) forest					
Bullhead Trail	7.6	√			6
Greenbrier Pinnacle Trail	9.0		√		
Red oak (chestnut) forest					
Greenbrier Pinnacle Trail	7.5				3
Thomas Divide, N.C.	10.0				2
Thomas Divide, N.C.	7.2				2
Pine heath					
Bullhead Trail	12.0	√	√		
Greenbrier Pinnacle Trail	10.0				3
Gray beech forest					
Double Springs Gap	7.6	√			
West of Siler's Bald	8.0		√		
Spruce-fir forest					
Climax, between Newfound Gap and Clingmans Dome	11.6	√	√		
Fraser fir, Clingmans Dome	6.8				2
Early seral, Mount Buckley	6.6	√			3
Mid-seral, Forney Ridge	5.6				3
Late seral, north of Andrews Bald	7.7				3
Heath bald					
Bullhead Trail	4.0				2
Brushy Mountain	10.0			2	

CENSUS AREAS

Pine-oak forest and sere.—The mature forest was an open stand of trees with a shrub layer of *Kalmia* and other Ericaceae. The ground was covered with a dry litter of pine and broad leaves. Two samples of a seral stage leading to the above forest contained both deciduous and pine trees, 1.8–6 m high, scattered through shrubs and open areas. Shrubs were predominantly greenbrier (*Smilax* spp.), smooth sumac (*Rhus glabra*) and briers (*Rubus* spp.). A luxurious growth of herbs covered most of the ground.

Cove forest.—All 5 areas censused were in the Greenbrier section of the Park. In 2 areas along Porters Creek, trees were widely spaced but made a deciduous canopy 25–45 m, occasionally 60 m, above the ground. Great rhododendron (*Rhododendron maximum*) made dense tangled thickets along the stream and herbs were luxuriant. The larger area had been censused by Aldrich and Goodrum (1946) the previous year. The 3 areas along Ramsey Prong are listed in ascending elevations. The lowest area had previously been cut over but had regained a closed canopy. The shrub layer in the highest area included sevenbark (*Hydrangea arborescens*) prominently, as well as rhododendron.

Mixed hemlock-deciduous forest.—Although eastern hemlock occurred prominently in the cove forest, it was the principal dominant in 3 areas censused. Hemlock attained diameters over 1 m and heights of 30 m. Beech formed an understory at low elevations and sweet (*Betula lenta*) and yellow (*B. allegheniensis*) birches at high elevations. Rhododendron and sevenbark were the principal shrubs. Herbs were much reduced compared with the cove forest, and the ground was covered with a thick layer of dry leaf litter.

Chestnut oak (chestnut) forest.—Trees in this forest rarely exceeded 0.5 m diameter and were usually only 6–18 m tall. Ericaceous shrubs were dense, especially at high elevations.

Red oak (chestnut) forest.—No tree counts were taken in this forest, but northern red oak was most prominent. The tree canopy was more closed than in the chestnut oak forest because of fewer dead chestnut trees and the shrub stratum was greatly reduced.

Pine heath.—Pines were widely spaced and only 6–12 m high. The shrub stratum was dense. The herb stratum was greatly reduced and contained bracken fern (*Pteridium* sp.) and some creeping vines.

Gray beech forest.—Beech (*Fagus grandifolia*) here is probably a different variety than occurs at low elevations (Camp 1950). Trees were generally 8–12 m tall, widely spaced and with intervening space covered with grasses, sedges and shrubs.

Spruce-fir forest and sere.—The climax forest contained dense tangles of mountain rose bay (*Rhododendron catawbiense*) and the ground was covered everywhere with thick spongy moss, low herbs and ferns. Numerous fallen trees were covered with mosses and lichens. At the highest elevation on Clingmans Dome, the forest consisted principally of Fraser fir (*Abies fraseri*) and included a few mountain ash (*Sorbus americana*) with the ground covered with thick mosses and *Oxalis*. Trees were numerous but only 12–15 m high.

A recently burned over area was well covered (90%) with shrubby vegetation, 0.6–1.5 m high, composed of fire cherry (*Prunus pennsylvanicus*), red maple (*Acer rubrum*), blackberry (*Rubus canadensis*), sevenbark, red-berried elder (*Sambucus pubens*) and several species of Ericaceae. Dead stubs of spruce and fir were scattered. The herb layer was dense and covered 70% of the ground. A second area, burned over earlier, had a dense stand of fire cherry, 1.8–3 m high. The area with most advanced vegetation, 3–6 m high, had serviceberry (*Amelanchier*), fire cherry, yellow birch and a few small spruce.

A heath bald along Bullhead Trail was covered mostly with mountain laurel (*Kalmia latifolia*) but contained some fire cherry and sourwood (*Oxydendrum arboreum*). The vegetation was dense and about 3 m high. Another heath bald on Brushy Mountain contained chiefly mountain rose bay 1–2 m high.

BIRD POPULATIONS

The data on species populations (Table 2) are listed in taxonomic order and the plant communities in which they were found. The plant communities are arranged as to whether they are seral or mature (climax), according to zones of altitude, and in horizontal gradients from north-facing slopes, coves, or gaps around the mountains to south-facing slopes.

Succession.—The shrubby seral stage at low elevations had a high percentage of restricted species and hence low S_s and S_p compared with either pine-oak or cove forest (Table 3). It likewise had little similarity with shrubby seral stages at high elevations. In contrast, the shrubby seral stages at high elevations had an avifauna with considerable similarity to that of the spruce-fir forest. Heath balds consist of very dense shrubby vegetation of uncertain successional status and contained only 3 species, none of them restricted: Gray Catbird (2.5 pairs/40 ha), Black-throated Blue Warbler (19 pairs), Rufous-sided Towhee (11 pairs).

Forest communities.—The forest contains both deciduous and coniferous species, in mixed or relatively pure stands, and with physiognomies varying from tall, luxuriant cove forest to short-statured gray beech "orchard" to open stands of pine heath. Relatively high S_s occurred among bird populations in cove, chestnut oak, red oak and hemlock-deciduous forests (Table 3). Likewise there was similarity between cove forest avifauna (after those species commonly associated with hemlock were eliminated) and pine-oak avifauna. Individual bird species extended widely among these deciduous plant communities although at different population levels.

When bird species commonly associated with deciduous trees were eliminated from the hemlock-deciduous forest, the remaining "hemlock" avifauna was similar to that of the spruce-fir forest. There was considerable similarity also between avifaunas of spruce-fir forest and high seral stages, even though these plant communities are of different vegetation types.

The avifauna of the pine heath was not closely similar to any other avifauna nor did any of its 14 species reach maximum population here. Many of its species occurred commonly in deciduous forests or shrub stages.

The above classification of avifaunas into separate units has been based largely on coefficients of S_s. However, no S_s above 50 has a value of S_p lower than 31, and no S_s below 50 has a value above 20.

Slope exposure (moisture).—North slopes and coves in the mountains are moist and shady, east and west slopes intermediate and south slopes dry and sunny. Correlated with changes in habitat is a continuum of plant

Table 2

Average Bird Populations (Pairs/40 Ha) in Different Types of Vegetation

Species	Bird community[a]	Pine-oak forest		Cove forest	Hemlock-deciduous forest	Chestnut oak (chestnut) forest	Red oak (chestnut) forest	Pine heath	Gray beech forest	Spruce-fir forest			
		seral	mature							early seral	mid-seral	late seral	climax
Ruffed Grouse *Bonasa umbellus*	DF			2.3	0.7	+[b]	3.0	+	5.0			5.0	+
Ruby-throated Hummingbird *Archilochus colubris*	FE		3.0	0.5		1.7							+
Common Flicker *Colaptes auratus*	FE	5.0		1.8	1.5	4.7		1.3					
Pileated Woodpecker *Dryocopus pileatus*	DF			0.5	3.0	2.5+							
Hairy Woodpecker *Dendrocopos villosus*	DF			3.0	2.7	1.3+	1.7		2.5	+			3.0
Downy Woodpecker *Dendrocopos pubescens*	DF	+	1.5+	1.1		+	3.3						
Great Crested Flycatcher *Myiarchus crinitus*	DF			0.5		11+	1.7						
Acadian Flycatcher *Empidonax virescens*	DF	+	5.0	2.0	5.0								
Eastern Wood Pewee *Contopus virens*	DF	4.0	1.5			+	1.7						
Blue Jay *Cyanocitta cristata*	FE			+	0.7	3.0+	3.3	1.3					
Black-capped Chickadee *Parus atricapillus*	DF			3.7	6.7	1.7	6.3	3.7			7.0	10.0	1.5
Carolina Chickadee *Parus carolinensis*	SM	3.7	1.0			6.7							

TABLE 2
Continued

Species	Bird community[a]	Pine-oak forest		Cove forest	Hemlock-deciduous forest	Chestnut oak (chestnut) forest	Red oak (chestnut) forest	Pine heath	Gray beech forest	Spruce-fir forest			
		seral	mature							early seral	mid-seral	late seral	climax
Tufted Titmouse													
Parus bicolor	DF		1.5+	0.5	+	5.3+							
White-breasted Nuthatch													
Sitta carolinensis	DF			+		+	3.7						
Red-breasted Nuthatch													
Sitta canadensis	BF				11.0			7.3				+	20.0
Brown Creeper													
Certhia familiaris	BF				4.0							5.0	38.0
Winter Wren													
Troglodytes troglodytes	BF			5.3	7.5					3.0	29.0	+	34.0
Carolina Wren													
Thryothorus ludovicianus	SM	1.3	+	2.1	+	+							
Gray Catbird													
Dumetella carolinensis	FE	5.0				+	2.0	2.0	2.5			5.0	
Brown Thrasher													
Toxostoma rufum	FE	4.3											
American Robin													
Turdus migratorius	FE				3.2		1.3		5.0	+	7.0		3.0
Wood Thrush													
Hylocichla mustelina	DF		3.0	29.0	18.0	5.3+	16.0						
Veery													
Catharus fuscescens	BF			0.6	8.7		15.0		28.0	21.0	14.0	26.0	18.0
Blue-gray Gnatcatcher													
Polioptila caerulea	SM		3.0										

TABLE 2
Continued

Species	Bird community[a]	Pine-oak forest		Cove forest	Hemlock-deciduous forest	Chestnut oak (chestnut) forest	Red oak (chestnut) forest	Pine heath	Gray beech forest	Spruce-fir forest			
		seral	mature							early seral	mid-seral	late seral	climax
Golden-crowned Kinglet													
Regulus satrapa	BF				2.5							5.0	38.0
White-eyed Vireo													
Vireo griseus	SM	14.0				3.3							
Yellow-throated Vireo													
Vireo flavifrons	DF	+	6.5										
Solitary Vireo													
Vireo solitarius	BF		1.5	25.0	36.0	+	7.7	+	22.0		7.0	5.0	24.0
Red-eyed Vireo													
Vireo olivaceus	DF	6.3	26.0	16.0	1.0	35.0	14.0						
Black-and-white Warbler													
Miniotilta varia	BF		8.5	3.0		13.0	3.0	+					
Worm-eating Warbler													
Helmitheros vermivorus	DF			1.1		10.0							
Golden-winged Warbler													
Vermivora chrysoptera	FE	12.0											
Parula Warbler													
Parula americana	SM		1.5										
Yellow Warbler													
Dendroica petechia	FE	5.3											
Black-throated Blue Warbler													
Dendroica caerulescens	BF			104.0	67.0	15.0	27.0	25.0	+	3.0	7.0	21.0	6.5
Black-throated Green Warbler													
Dendroica virens	BF			8.8	50.0	5.3	1.3						+

TABLE 2
Continued

Species	Bird community[a]	Pine-oak forest		Cove forest	Hemlock-deciduous forest	Chestnut oak (chestnut) forest	Red oak (chestnut) forest	Pine heath	Gray beech forest	Spruce-fir forest			
		seral	mature							early seral	mid-seral	late seral	climax
Blackburnian Warbler													
Dendroica fusca	BF			1.0	41.0								
Yellow-throated Warbler													
Dendroica dominica	SM		30.0										
Chestnut-sided Warbler													
Dendroica pennsylvanica	BF					1.7+	19.0	24.0	46.0	141.0	115.0	47.0	2.5
Pine Warbler													
Dendroica pinus	SM		18.0										
Prairie Warbler													
Dendroica discolor	SM	15.0											
Ovenbird													
Seiurus aurocapillus	DF		16.0	15.0	36.0	29.0	28.0	1.3	2.5				
Louisiana Waterthrush													
Seiurus motacilla	DF	1.3		+									
Kentucky Warbler													
Oporornis formosus	SM	3.7		0.5		7.3							
Common Yellowthroat													
Geothlypis trichas	FE	12.0								27.0			
Yellow-breasted Chat													
Icteria virens	FE	24.0				1.7							
Hooded Warbler													
Wilsonia citrina	DF		10.0	1.0		32.0	3.3	4.7					
Canada Warbler													
Wilsonia canadensis	BF			6.3	32.0		5.0		2.5	6.0+	22.0	21.0	

TABLE 2
Continued

Species	Bird community[a]	Pine-oak forest		Cove forest	Hemlock-deciduous forest	Chestnut oak (chestnut) forest	Red oak (chestnut) forest	Pine heath	Gray beech forest	Spruce-fir forest			
		seral	mature							early seral	mid-seral	late seral	climax
American Redstart													
Setophaga ruticilla	DF	1.3	+	+									
Scarlet Tanager													
Piranga olivacea	DF		1.5	9.8	5.0	15.0	6.7	+					
Summer Tanager													
Piranga rubra	SM		1.5										
Cardinal													
Cardinalis cardinalis	SM	3.0	+			1.7							
Rose-breasted Grosbeak													
Pheucticus ludovicianus	DF				2.5	+	1.3		2.5				
Indigo Bunting													
Passerina cyanea	FE	22.0								+			
Rufous-sided Towhee													
Pipilo erythrophthalmus	FE	12.0	+			34.0	5.3	37.0	2.5	66.0	22.0	5.0	
Dark-eyed Junco													
Junco hyemalis	BF			9.7	30.0		23.0		56.0	102.0	58.0	83.0	125.0
Field Sparrow													
Spizella pusilla	FE	17.0								+			

[a] Bird communities: SM, southeastern mixed; DF, deciduous forest; FE, forest-edge; BF, boreal forest.
[b] Population below 0.5 pair/40 ha.

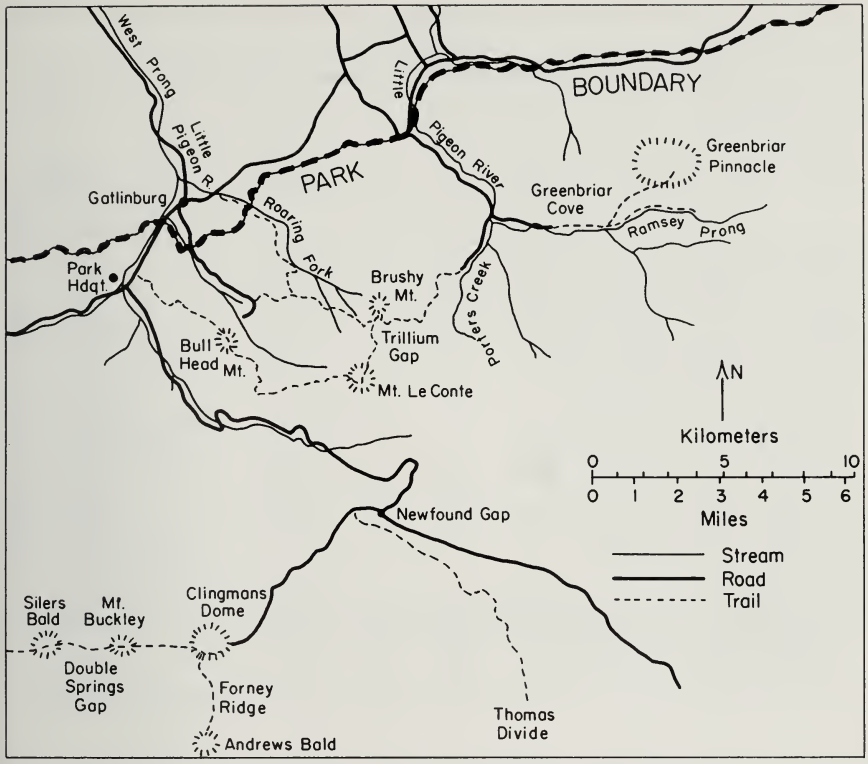


FIG. 2. Map of region in which census areas were located.

communities. At low elevations, there was no observable difference between total bird species and total pairs between cove and hemlock-deciduous forests on north slopes and chestnut oak on intermediate slopes, but fewer species and smaller populations occurred in pine-oak forests on south slopes (Table 4). At higher elevations, there was an observable decrease in both total species and pairs from red oak forests on intermediate slopes to pine heath on exposed south slopes.

Bond (1957), working in southern Wisconsin with a continuum of plant communities in the ecotone between grassland and deciduous forest, found an increase in number of bird species and total populations from moist to intermediate stages and then a decline to the dry end. Individual species varied in their point of greatest abundance along the gradient. Likewise, Smith (1977) observed 3 of the 8 species studied restricted to the moist end of a deciduous forest continuum in the Ozark Mountains of Arkansas and only 1 species extending to the extreme dry end.

TABLE 3

COMPARISON OF SPECIES COMPOSITION AND POPULATIONS BETWEEN COMMUNITIES

Communities compared	Restricted species: 1st community N	Restricted species: 1st community %	Restricted species: 2nd community N	Restricted species: 2nd community %	Similarity indices S_s	Similarity indices S_p
Low seral stage: pine-oak forest	13	57	13	57	44	5
Low seral stage: cove forest	8	35	23	74	30	5
Low seral stage: high and early mid-seral stages	19	83	10	71	22	10
High seral stages: spruce-fir forest	5	36	6	40	62	40
Cove forest: chestnut oak forest	8	26	9	28	73	31
Chestnut oak forest: red oak forest	11	34	4	16	74	41
Cove forest: gray beech forest	23	74	5	38	36	20
Gray beech forest: high seral stages	2	15	8	42	69	58
Cove forest: hemlock-deciduous forest	10	32	5	19	74	55
Cove forest: spruce-fir forest	21	68	5	33	22	18
"Hemlock" forest[a]: spruce-fir forest	2	13	2	13	87	34
Pine heath: spruce-fir forest	8	57	9	60	21	9
Pine heath: pine-oak forest	8	57	17	74	32	5
Pine-oak forest: "deciduous cove forest"[b]	10	44	10	44	56	35

[a] "Deciduous forest bird species" eliminated from the hemlock-deciduous forest.
[b] "Hemlock bird species" eliminated.

Elevation.—Increase in altitude or elevation brings lower temperatures, more precipitation including snowfall, shorter growing seasons, greater wind velocities, and more cloudiness and fog (Shanks 1954).

Vertical ranges of the Black-capped and Carolina chickadees overlapped in the chestnut oak (chestnut) forest (Table 5), but the Black-capped was there only in 1947 and the Carolina Chickadee only in 1948. The 2 species have nearly identical territorial requirements, and competitive interrelations of the two are well established (Tanner 1952, Brewer 1963).

The Wood Thrush and Veery overlapped broadly in vertical distribution and in the same census plots. Cavanaugh and Magee (1967) observed that when 1 species was numerous in a mixed coniferous-deciduous forest, the other was less so with the situation reversing in another year, which indicated the possibility of conflict between them. Bent (1949) cited several instances of the Veery and American Robin being driven from their territories by the Wood Thrush, and he observed a Veery driving a Wood Thrush from its territory. Bertin (1977) suggested that in mixed forest

TABLE 4

STATISTICS ON BIRD POPULATIONS IN PLANT COMMUNITIES

Plant community	Elevation (m)	Total species	Total pairs	Species diversity H'	Equitability J'	Pairs per species: mean p/s	Pairs per species: median p/s	Pairs per species: skewness g_1
Pine-oak forest								
Seral	455–488	23	172+	2.707	0.904	7.5	5.0	0.99
Mature	411–488	23	140+	2.397	0.814	6.1	1.6	1.8
Cove forest	640–1250	31	254+	2.206	0.669	8.2	2.0	4.5
Hemlock-deciduous forest	873–1356	26	376+	2.574	0.810	14.5	5.0	1.4
Chestnut oak (chestnut) forest	817–1074	32	247+	2.706	0.851	7.7	3.2	1.7
Red oak (chestnut) forest	1222–1506	25	204	2.762	0.858	8.2	3.7	1.3
Pine heath	1219–1349	14	108+	1.707	0.741	7.7	1.6	1.7
Gray beech forest	1646–1713	13	177+	1.821	0.733	13.6	2.6	1.5
Spruce-fir forest								
Early seral	1890–1950	12	369+	1.527	0.734	30.8	4.5	1.6
Mid-seral	1798–1920	10	288	1.824	0.792	28.8	18.0	2.2
Late seral	1740–1795	14	328+	1.974	0.794	17.0	5.0	2.2
Climax	1760–1790	15	314+	1.889	0.760	20.9	6.5	2.7

the Veery may segregate into sites with cooler microclimates than those preferred by the Wood Thrush.

Yellow-throated, Red-eyed and Solitary vireos were all present in pine-oak plots and Red-eyed and Solitary vireos occurred in red oak (chestnut) at higher elevations. The Yellow-throated Vireo feeds and nests in both deciduous and pine trees and may be a competitor of the Solitary Vireo in the pine forests of the Piedmont region (Odum 1948). Both Solitary and Red-eyed vireos were abundant in the cove forest but only the Solitary Vireo occurred in the hemlock forest. The Solitary Vireo commonly sang and fed in both deciduous and coniferous trees from 2 m–ca. 12 m above the ground. The Red-eyed Vireo was never observed in coniferous trees and in deciduous trees carried on its activities from 2 m above ground to the tree tops. This agrees in general with observations of the 2 species in mixed forests in New York state (Kendeigh 1945).

The vertical ranges of the 2 nuthatches broadly overlapped but the White-breasted Nuthatch was largely confined to deciduous stands and the Red-breasted Nuthatch to coniferous ones. The ranges of warbler species from the upper and lower elevations did not overlap except for the Hooded and Canada warblers in the cove forest.

Table 5

Vertical Distribution of Congeneric Species in the Great Smoky Mountains

Low elevation species	Highest elevation reached (m)	Congeneric species	High elevation species	Lowest elevation reached (m)	Congeneric species
Carolina Chickadee	817–1045	absent	Black-capped Chickadee	732–802	absent
White-breasted Nuthatch	1415–1506	absent	Red-breasted Nuthatch	873–991	absent
Wood Thrush	1451–1506	present	Veery	899–975	present
White-eyed Vireo	488	absent			
Yellow-throated Vireo	411–488	present	Solitary Vireo	411–488	present
Red-eyed Vireo	1222–1318	present	Solitary Vireo	411–488	present
Yellow Warbler	488	absent			
Prairie Warbler	488	absent			
Yellow-throated Warbler	411–488	absent	Black-throated Blue Warbler	640–820	absent
Pine Warbler	411–488	absent	Black-throated Green Warbler	640–820	absent
			Blackburnian Warbler	732–802	absent
Hooded Warbler	1295–1343	absent	Canada Warbler	899–975	present
Summer Tanager	411–488	absent	Scarlet Tanager	411–488	absent

Summer and Scarlet tanagers both occurred in the pine-oak census plot but in different years. Stupka (1963) states that the 2 species commonly meet at 457–610 m.

DISCUSSION

Local factors.—The predominant factor controlling bird distribution in the Great Smoky Mountains is the relation of bird species to plant communities. The change in moisture gradients from north to south slopes and temperature gradients with elevation are of secondary importance. Plant communities are identified by life forms of their dominant plant species (deciduous tree, coniferous tree, shrub), physiognomy (dense closed forest, open forest, heath), location (cove, bald) and species composition. Each plant community, or at least vegetation type, provides a different environment for birds with respect to microclimate (modification of the macroclimate), plant structure (dimensions, branching, leaf size and arrangement) and food supplies (seeds, nuts, fruit, foliage, insects and other invertebrates). Each bird species has evolved adjustments to these factors but little new information concerning their precise niche requirements and role in the community can be provided beyond those discussed for many of these species by Kendeigh (1945, 1947), MacArthur (1958), James (1971), Anderson and Shugart (1974) and Rabenold (1978).

The difference in bird species composition between seral shrubs and mature pine-oak forest at low elevation appears clearly related to change in life form of the conspicuous plants and the physiognomy of their stands. Forest species with the largest populations are segregated into either deciduous or needle-leaved coniferous vegetation types.

Food resources may be a factor affecting population size. Whittaker (1952) has shown that productivity of foliage insects in the Great Smoky Mountains decreases with slope exposure from moist cove forests to dry oak and pine types and with elevation. Bond (1957) found that foliage insect gleaners decreased and plant feeders increased from moist to dry forests in Wisconsin.

Circumstantial evidence indicated that competition as well as changes in vegetation affected vertical limits of some species in the Great Smoky Mountains. Able and Noon (1976) found no convincing cases of altitudinal competitive exclusion between species in the temperate mountain forests of New York and Vermont. Upper and lower distributional limits of species coincided with ecotones in vegetation. In the tropical forests of New Guinea, Diamond (1973) believed competition to be more important than changes in vegetation in controlling vertical distribution. In the tropical mountains of Peru, Terborgh (1971) ascribed changes in vegetation to account for less than 20% of the altitudinal limits of species, competition for about 33%

and gradually changing physical and other biological conditions for about 50%. Included in this latter category were not only changes in temperature and cloudiness, but also changes in net annual plant productivity, density of insects and importance of epiphytic plants in the vegetation.

Geography.—Avifaunas in similar plant communities at different localities tend to be similar in species composition (S_s) but not identical. Of 301 species recorded in 6 comparisons of localities (Table 6), 62% occurred in both communities, 21% were found in other plant communities in the vicinity, 11% were absent because the locality was beyond their geographic ranges, while 6% were not recorded in the locality. Failure to record a species in a locality within its distributional range may indicate that the sampling area was too small, and this may also be partly responsible for finding species only in other plant communities.

Other factors, however, often affect local occurrence of species. For instance, presence of Red-breasted Nuthatch, Brown Creeper, Winter Wren and Golden-crowned Kinglet in hemlock communities in the Great Smoky Mountains and not on the Heldenberg Plateau of New York may represent an overflow from large populations of these species in nearby spruce-fir communities. In New York state, spruce-fir forests are separated by 25–60 km from the hemlock areas censused. Another local factor is the presence of competing species. In hemlock-deciduous forests on the Highlands Plateau of North Carolina, the Carolina Chickadee replaces the Black-capped Chickadee.

The bird species composition varies, of course, when the plant community is beyond the limit of distribution of the bird species. The Scarlet Tanager was not recorded in the pine-oak community on the Piedmont Plateau of Georgia because it is rare or absent there; the Brown-headed Nuthatch (*Sitta pusilla*) recorded in the Georgia area is rare or absent in the Great Smoky Mountains. Nineteen species found in spruce-fir forests of northern Maine do not extend their ranges south as far as the Great Smoky Mountains. The decrease in species richness in Appalachian spruce-fir forests from north to south is a progressive one (Rabenold 1978).

Coefficients of population similarity, S_p, were not used in these comparisons of avifaunas. They are more sensitive indicators of similarity because they depend not only on the presence or absence of a species as does S_s, but on the replication of identical characteristics of the environment to permit equal sized populations to develop. Populations may also vary locally in sex and age ratios and other properties that would affect realization of comparable population sizes. In our comparisons of avifaunas in different localities, there was an additional complication in that censuses were taken in different years, and population sizes in a locality fluctuate from year to year.

Table 6

Geographic Comparison of Avifaunas

Locality	Distance (km)	Species similarity S_s	Species in common	Restricted species at other locality: In other plant communities	Restricted species at other locality: Beyond distributional range	Restricted species at other locality: Not recorded	Pairs/species: Mean p/s	Pairs/species: Median p/s	Pairs/species: Skewness g_1	Authority
Pine-oak, pine forests										
Great Smoky Mountains	—	—	17	2	1	3	6.1	1.6	1.8	this study
Piedmont Plateau, Georgia	160	67	17	8	1	3	6.9	5.0	3.2	Johnstone and Odum 1956
Chestnut oak, red oak forests										
Great Smoky Mountains	—	—	18	10	3	5	7.7	3.2	1.7	this study
Highlands Plateau, North Carolina	60	67	18	0	0	0	8.9	4.0	1.9	Odum 1950
Hemlock-deciduous forests										
Great Smoky Mountains	—	—	17	1	4	4	14.5	5.0	1.4	this study
Highlands Plateau, North Carolina	60	63	17	11	0	0	10.7	5.0	2.1	Odum 1950
Great Smoky Mountains	—	—	15	8	3	0	14.5	5.0	1.4	this study
Helderberg Plateau, New York	1100	62	15	4	2	1	7.5	4.0	1.8	Kendeigh 1946
Spruce-fir forests										
Great Smoky Mountains	—	—	14	0	0	1	20.9	6.5	2.7	this study
Great Smoky Mountains	25	80	14	5	0	1	14.0	8.0	2.0	Alsop 1969
Greak Smoky Mountains	—	—	13	1	1	0	20.9	6.5	2.7	this study
Aroostock County, Maine	1800	44	13	12	19	0	7.9	10.0	3.2	Stewart and Aldrich 1952

Bird communities, their origins and history.—Hubbard (1971) has a general discussion of the origins of avifaunas in the southern Appalachians but we wish to consider these origins and history from a somewhat different viewpoint. Our analysis above of succession, forest communities, and geography shows considerable similarity in the species composition of avifaunas that occur in plant communities of the same vegetation type, particularly deciduous forest, needle-leaved coniferous forest and shrubby vegetation at low elevations. Each combination of avifaunas in the same vegetation type or bird community shows little similarity to either of the others (Table 3). "Preference" of bird species for particular types of vegetation is indicated by maximum populations being attained in them. Such maximum populations suggest a high degree of anatomical, physiological and behavioral adaptation through association with the vegetation over a long period of geological time. In Table 2, each species is assigned to the bird community to which it most characteristically belongs, although most species have enough flexibility that they occur in small numbers in other communities as well. Much concerning the origin and geological history of each bird community can be learned from the presence of associated plant species in the fossil record of various localities and times, as was traced by Kendeigh (1974).

The uniqueness of the low elevation shrub avifauna is the result of intermingling of bird species belonging to the deciduous forest-edge community (FE) and what we have called the southeastern mixed community (SM). Belonging to this latter are the southern pines and several bird species found in the pine-oak community. This vegetation is derived from the Madro-Tertiary Geoflora originating on the Mexican Plateau, which during the Miocene or earlier extended continuously around the Gulf of Mexico. The southeastern portion and its avifauna became separated when prairie vegetation penetrated to the Gulf of Mexico.

The deciduous forest (DF) and forest-edge (FE) communities are derived from the temperate unit of the Arcto-Tertiary Geoflora that during the Eocene epoch extended from southeastern United States to Alaska (Kendeigh 1974). This forest and its seral stages have been much buffeted by climatic changes during the last 65 million years and are now largely limited to the eastern United States. The mixed mesophytic forest of the southern Appalachian Mountains, best represented here by the cove forest, has been little affected by these changes and may be the oldest forest stand at any locality in temperate North America (Braun 1950).

The gray beech forest, unique to the Appalachian Mountain System, is a segregate from the mixed mesophytic forest (Braun 1950). It is a young forest geologically, and since it is subjected to more climatic stresses than the deciduous forest at lower elevations, only a few bird species from the

deciduous forest community have been able to occupy it. Instead, it has become occupied by species from the spruce-fir coniferous forest community.

Seral stages at high elevations became extensive only in recent times as the result of fires and human disturbances. Although a few species have invaded from shrubby seral stages of the lowlands, most of the avifauna is of boreal origin. There are no unique species here, although the Veery and Chestnut-sided Warbler reach peak populations in this vegetation and in the gray beech forest.

The spruce-fir forest (BF) is derived mainly from the boreal unit of the Arcto-Tertiary Geoflora (Kendeigh 1974). In the early Tertiary period, this unit was widely spread over northern North America. During the Pleistocene epoch it became fragmented, with the eastern portion becoming restricted and isolated in the northeastern United States and south through the Appalachian Mountains. During the height of glaciation, the spruce-fir forest in the Great Smoky Mountains probably extended to lower elevations and occupied mountain tops farther south than at present. During the warm dry xerothermic period, beginning some 8000–9000 years ago following the retreat of the last major or Wisconsin glacier, this forest retreated to higher elevations and became eliminated from lower peaks south of Clingmans Dome. During this period the southern distributional limits of many bird species probably retreated northward. The cooler, moister climate of the last 2000–3000 years may have again permitted the spruce-fir forest to expand down the slopes and bird species to extend their ranges southward. The gray beech forest probably originated during these up and down movements of the vegetation (Whittaker 1956).

The eastern hemlock forest lies geographically between boreal and deciduous forests but occurs more often in mixed stands with deciduous trees than with spruce and fir. It was subjected to several contractions and extensions of range during the Pleistocene and Holocene epochs. It differs from the boreal forest in the luxurious development of rhododendron and other shrubs in the Appalachian Mountain System, which together with a more temperate and moist climate presents a somewhat different environment for birds. This has led to a secondary differentiation of its avifauna from that of the spruce-fir forest which is more evident when the 2 forests are some distance apart, as on the Helderberg Plateau of New York, than in the Great Smoky Mountains. Other variations in avifaunas of the boreal forest have been described by Erskine (1977).

The fact that 2 species in hemlock forests of New York and 19 species in spruce-fir forests of Maine were not found as breeding birds in the Great Smoky Mountains may be the result, in part, of these historical shifts in the vegetation. Since the last contraction of their ranges northward, time

may not have been sufficient for them to reoccupy southward all favorable breeding areas that have become available. These areas are scattered and require even migratory bird species to jump from one mountain to another for breeding purposes. For example, Golden-crowned Kinglet, Winter Wren, Black-capped Chickadee and Black-throated Green Warbler, although common in the Great Smoky Mountains, were not found in the census areas on the Highlands Plateau of the Blue Ridge Mountains. The Black-throated Green Warbler is of special interest as the Highlands Plateau lies in a hiatus between the ranges of the subspecies in the mountains (*Dendroica v. virens*) and the coastal subspecies (*D. v. waynei*). Odum (1950) has suggested that in dispersal of the species southward, the ranges of the mountain population became split from the coastal population and that the plateau has not yet become occupied by the mountain race.

In addition to slow dispersal rates southward, restriction of species southward may also be in response to unfavorable climate, food resources, or inter-species competition. Rabenold (1978) ignores the probable influence of the post-glacial xerothermic period on bird distribution in the Appalachians and argues that the lower species richness is related to lower food levels during the reproductive season.

Community structure.—The structure of bird communities is commonly analyzed in terms of species richness (s), equitability or eveness of distribution of populations (J') and segregation of species into different niches. The first 2 factors are usually combined into a species diversity index (H'). We are not here concerned with analysis of ecological niches. In our data (Table 4), H' varied positively with s ($r = 0.87$, $P < 0.001$) but J' varied independently of s. We agree with Hurlbert (1971) that the usefulness of H' is limited. There is little advantage in combining the 2 components.

Levels of population size attained by different species in communities or areas is important. Where the distribution of different population sizes follows a normal or Gaussian curve, mean number of pairs per species (p/s) is a reliable estimate. In each of our plant communities, however, the distribution of populations was skewed in that the median population was less than the mean, and the mode, usually poorly defined, was less than the median. The difference (± SD) between the mean and median p/s averaged 65 ± 17% of the mean. The degree to which distribution of populations was skewed (g_1) is indicated in Table 4, all populations being significantly different from symmetrical ($P < 0.05$), although that of the seral stage to pine-oak forest ($g_1 = 0.99$) was borderline.

There is a highly significant negative correlation between g_1 and J' ($r = 0.69$, $P < 0.0025$). A high value of g_1 and a low value of J' both indicate wide scattering of p/s, hence there is no need to use both indices. The distribution of measurements of biological variables commonly adheres to

a normal curve, and since g_1 indicates the departure from symmetry it is preferable to J' which indicates departure from equality, which is rare or absent in biological phenomena.

P/s varied negatively with *s* ($r = 0.69$, $P < 0.025$) and this was related to altitude. At elevations below 1600 m, average *s* per community was 25 and *p/s* 8.6; above 1600 m, *s* was 13 and *p/s* 22.2. Skewness, g_1, was not statistically correlated with *s* and varied from 0.99 in the seral shrub stage to 4.5 in the cove forest, both at low elevations (Table 4). If the cove forest is excluded for reasons given beyond, g_1 averaged 1.5 below and 2.0 above 1600 m. At 1800 m elsewhere in the Great Smoky Mountains, *s*, *p/s* and g_1 values were intermediate (Table 6, Alsop 1969). In spruce-fir forests occurring at low elevations in Maine, *s* was higher and *p/s* lower than in the spruce-fir forest at high elevation in the Great Smoky Mountains, but g_1 was higher (Table 6). At both low and high elevations, g_1 was lower in seral shrubby stages than in forests (Table 4). Able and Noon (1976) state that decreasing *s* and increasing *p/s* with elevation seem to be a general rule in forested regions. Other investigators agree that fewer species and greater variability in population size tend to occur in rigorous environments with variable weather and other conditions than in moderate ones (Tramer 1969, Kricher 1972, Rotenberry 1978, Rotenberry et al. 1979).

The considerably skewed distribution of populations in the cove forest ($g_1 = 4.5$) is caused by 1 of the 31 species present, Black-throated Blue Warbler, having 41% of the total number of pairs. This species sings, nests and feeds in rhododendron and other ericaceous shrubs and in the rich herbaceous stratum. *Rhodendron maximum* is a characteristic dominant in the undergrowth of southern Appalachian Mountains but very local or absent from mixed mesophytic forests elsewhere (Braun 1950). The warbler has exploited this special niche and without effective competition from other species, its population has exploded in size. The high g_1 of hemlock-deciduous forests on the Highlands Plateau of North Carolina (Table 6) was also caused by the predominance of this species.

High values of g_1 found in gray beech and high elevation mid- and late seral communities are correlated with exploitation of favorable local niches by the Dark-eyed Junco and Chestnut-sided Warbler. The early seral stage has even larger populations of these 2 species, but g_1 is lower because 3 other species also have large populations so as to give a better balance among the 12 species that occur. The climax spruce-fir forest has several species with large populations, but g_1 is high because the Dark-eyed Junco comprised 40% of the total. Inter-species competition is reduced in these high elevation communities because other potentially competitive boreal species have not extended their ranges this far south.

The high g_1 for pine forests on the Piedmont Plateau of Georgia (Table

6) resulted from the Pine Warbler constituting 25% of the total populations of all 29 species. Pine Warblers nest and feed in long-leaved pines.

In the spruce-fir forest of Maine, the high g_1 resulted from Bay-breasted (*Dendroica castanea*) and Magnolia (*D. magnolia*) warblers making up 30% of total populations even with 44 species present. This may be a temporary unbalance, however, as these species were favored by feeding on the spruce budworm insect infestation then in progress.

Pairs per species (*p/s*) in hemlock-deciduous and spruce-fir forests of the Great Smoky Mountains are higher and in the chestnut oak and red oak forests lower than at other localities (Table 6). In each comparison, *p/s* varied inversely with *s*. It appears that when few species are present the fundamental niches for at least some species may be almost fully occupied so that populations are large. On the other hand, with many species present to provide inter-species competition, realized niches are smaller, hence smaller populations.

SUMMARY

Species composition and population sizes of birds were determined in 12 plant communities of the Great Smoky Mountains during the summers of 1947 and 1948. Plant communities form a mosaic of seral and climax stages that varies with altitude and slope exposure.

Coefficients of species and population similarities indicated that distinct bird communities may be identified, associated with deciduous forest, forest-edge, boreal forest and a southeastern mixed complex. Each type of vegetation with its bird life has had a different geological history that affects its present composition and characteristics. Bird species are classified to the vegetation type to which they appear best adapted as indicated by their attainment of highest populations.

Composition of bird species within particular stands of a vegetation type is influenced by the location of the stand in respect to species' ranges, neighboring avifaunas, annual fluctuations (especially of the less common species), inter-species competition and responses to temperature and possibly moisture as determined by elevation and slope exposure.

The species diversity index (H') varied positively with species richness (s) and was of limited value in comparing bird populations. Distributions of bird population sizes in all plant communities was positively skewed. Skewness (g_1) varied negatively with (J') and is preferred as an index as it indicates degree of departure from a symmetrical distribution rather than from equal population sizes of species.

Increasing elevation was correlated with lower species richness (s), larger number of pairs per species (p/s) and a tendency toward higher g_1, although the latter also varied independently of altitude. Avifaunas with g_1 greater than 2.0 contained one or more species with high abundance resulting from local prevalence of favored vegetation niches and lack of inter-species competition or with temporary super-abundance of a food resource. Values of p/s may be compared when the g_1 of avifaunas are similar. P/s varied negatively with s, indicating that with larger number of species present, inter-species competition caused fundamental niches not to be fully realized, with the consequence that growth of populations for individual species was limited.

ACKNOWLEDGMENTS

The junior author was responsible for the fieldwork and a preliminary analysis of data for

his doctorate thesis at the University of Illinois. The senior author revised and up-dated the manuscript. We are grateful to Robert H. Whittaker for providing vegetation analyses for several of the census areas and for cooperation in other ways and to Arthur Stupka, at that time Park Naturalist, for pointing out and providing access to suitable study areas in the various types of vegetation. James R. Karr, Frances C. James, James F. Parnell and Jerrold H. Zar provided helpful comments on early drafts of the manuscript.

LITERATURE CITED

Able, K. P. and B. R. Noon. 1976. Avian community structure along elevational gradients in the northeastern United States. Oecologia (Berl.) 26:275–295.

Aldrich, J. W. and P. Goodrum. 1946. Tenth breeding bird census: virgin hardwood forest. Audubon Mag. 48:144–145.

Alsop, F. J., III. 1969. Thirty-third breeding bird census: virgin spruce-fir forest. Audubon Field Notes 23:716.

Anderson, S. H. and H. H. Shugart, Jr. 1974. Habitat selection of breeding birds in an east Tennessee deciduous forest. Ecology 55:828–837.

Bent, A. C. 1949. Life histories of North American thrushes, kinglets, and their allies. U.S. Natl. Mus. Bull. 196.

Bertin, R. I. 1977. Breeding habitats of the Wood Thrush and Veery. Condor 79:303–311.

Bond, R. R. 1957. Ecological distribution of breeding birds in the upland forests of southern Wisconsin. Ecol. Monogr. 27:351–384.

Braun, E. L. 1950. Deciduous forests of eastern North America. The Blakiston Co., Philadelphia, Pennsylvania.

Brewer, R. 1963. Ecological and reproductive relationships of Black-capped and Carolina chickadees. Auk 80:9–47.

Camp, W. H. 1950. A biogeographic and paragenetic analysis of the American beech (*Fagus*). Am. Philos. Soc. Yearbook 1950:166–169.

Cavanaugh, J. and A. Magee. 1967. Thirty-first breeding bird census: climax hemlock-white pine forest, with transitional hardwood. Audubon Field Notes 21:626–627.

Diamond, J. M. 1973. Distributional ecology of New Guinea birds. Science 179(4075):759–769.

Erskine, A. J. 1977. Birds in boreal Canada: communities, densities and adaptations. Canadian Wildl. Serv., Rept. Ser. 41:1–71.

Fawver, B. J. 1950. An analysis of the ecological distribution of breeding bird populations in eastern North America. Ph.D. thesis, Univ. Illinois, Champaign, Illinois.

Hubbard, J. P. 1971. The avifauna of the southern Appalachians: past and present. Pp. 197–232 *in* The distributional history of the biota of the southern Appalachians, Pt. III, Vertebrates (P. C. Holt, ed.). Virginia Polytechnic Inst. and State Univ., Res. Div. Monogr. 4, Blacksburg, Virginia.

Hurlbert, S. H. 1971. The nonconcept of species diversity: a critique and alternative explanations. Ecology 52:577–586.

James, F. C. 1971. Ordinations of habitat relationships among breeding birds. Wilson Bull. 83:215–236.

Johnstone, D. W. and E. P. Odum. 1956. Breeding bird populations in relation to plant succession on the Piedmont of Georgia. Ecology 37:50–62.

Kendeigh, S. C. 1945. Community selection by birds on the Helderberg Plateau of New York. Auk 62:418–436.

———. 1946. Breeding birds of the beech-maple-hemlock community. Ecology 27:226–244.

———. 1947. Bird population studies in the coniferous forest biome during a spruce budworm outbreak. Dept. Lands and Forests Ontario, Canada, Div. Res., Biol. Bull. 1:1–100.

———. 1974. Ecology with special reference to animals and man. Prentice-Hall, Inc., Englewood Cliffs, New Jersey.

KRICHER, J. C. 1972. Bird species diversity: the effect of species richness and equitability on the diversity index. Ecology 53:278–282.

MACARTHUR, R. H. 1958. Population ecology of some warblers of northeastern coniferous forests. Ecology 39:599–619.

ODUM, E. P. 1948. Nesting of the Mountain Vireo at Athens, Georgia, conclusive evidence of a southward invasion. Oriole 13:17–20.

———. 1950. Bird populations of the Highlands (North Carolina) Plateau in relation to plant succession and avian invasion. Ecology 31:587–605.

PALMGREN, P. 1930. Quantitative Untersuchungen über die Vogelfauna in den Wäldern Südfinnlands mit besonderer Berücksuchtingung Älands. Acta. Zool. Fenn. 7:1–219.

PIELOU, E. C. 1966. The measurement of diversity in different types of biological conditions. J. Theoret. Biol. 13:131–144.

RABENOLD, K. N. 1978. Foraging strategies, diversity, and seasonality in bird communities of Appalachian spruce-fir forests. Ecol. Monogr. 48:397–424.

ROTENBERRY, J. T. 1978. Components of avian diversity along a multifactorial climatic gradient. Ecology 59:693–699.

———, R. E. FITZNER AND W. H. RICKARD. 1979. Seasonal variation in avian community structure: differences in mechanisms regulating diversity. Auk 96:499–505.

SHANKS, R. E. 1954. Climates of the Great Smoky Mountains. Ecology 35:354–361.

SHELDON, A. L. 1969. Equitability indices: dependence on the species count. Ecology 50:466–467.

SMITH, K. G. 1977. Distribution of summer birds along a forest moisture gradient in an Ozark watershed. Ecology 58:810–819.

STEWART, R. E. AND J. W. ALDRICH. 1952. Ecological studies of breeding bird populations in northern Maine. Ecology 33:226–238.

STUPKA, A. 1963. Notes on the birds of Great Smoky Mountains National Park. Univ. Tennessee Press, Kingsport, Tennessee.

TANNER, J. R. 1952. Black-capped and Carolina chickadees in the southern Appalachian Mountains. Auk 69:407–424.

TERBORGH, J. 1971. Distribution on environmental gradients: theory and a preliminary interpretation of distributional patterns in the avifauna of the Cordillera Vilcabamba, Peru. Ecology 52:23–40.

TRAMER, E. J. 1969. Bird species diversity: components of Shannon's formula. Ecology 50:927–929.

WHITTAKER, R. H. 1952. A study of summer foliage insect communities in the Great Smoky Mountains. Ecol. Monogr. 22:1–44.

———. 1956. Vegetation of the Great Smoky Mountains. Ecol. Monogr. 26:1–80.

ZAR, J. H. 1974. Biostatistical analysis. Prentice-Hall, Inc., Englewood Cliffs, New Jersey.

VIVARIUM BLDG., UNIV. ILLINOIS, CHAMPAIGN, ILLINOIS 61820 AND BIOLOGY DEPT., SOUTHWESTERN OREGON COLL., COOS BAY, OREGON 97420. ACCEPTED 1 MAY 1980.

Wilson Bull., 93(2), 1981, pp. 243–248

NEST-SITE SELECTION AMONG ADÉLIE, CHINSTRAP AND GENTOO PENGUINS IN MIXED SPECIES ROOKERIES

Nicholas J. Volkman and Wayne Trivelpiece

The literature on pygoscelid penguins, the Adélie (*Pygoscelis adeliae*), the Chinstrap (*P. antarctica*) and the Gentoo (*P. papua*) penguins, is replete with statements about their nest-site preferences (Clarke 1906, Murphy 1936, Conroy et al. 1975, Muller-Schwarze and Muller-Schwarze 1975, White and Conroy 1975). Similar cohabiting avian species might be expected to develop specific habitat preferences (Klopfer and Hailman 1965) and some authors (White and Conroy 1975, Muller-Schwarze and Muller-Schwarze 1975) have suggested that sympatrically breeding pygoscelid penguins have nest-site preferences. However, these preferences have never been quantified. The purpose of this study was to quantitatively describe the nest-sites selected by sympatrically breeding Adélie, Chinstrap and Gentoo penguins.

METHODS

All 3 pygoscelids breed in 2 rookeries (after Penney 1968) located near Point Thomas (62°10′S, 58°30′W), King George Island, South Shetland Islands. The rookeries are separated by a glacial tongue, 3 km wide. The Polish Academy of Sciences Antarctic Station, Henryk Arctowski, is located 1 km from the west rookery. Data were collected between 1 November 1977 and 21 February 1978.

A census of penguin colonies (after Penney 1968) was conducted in both rookeries 1–2 weeks following peak egg-laying of each species. Individual counts were made of gentoo and chinstrap nest-sites. Adélie nests were counted individually in colonies of fewer than 150 pairs, and were estimated in larger colonies by determining the colony's area and using the figure of 1.13 pairs/m^2 obtained from small colonies (Trivelpiece and Volkman 1979).

The majority of measurements were taken on penguin colonies in the west rookery, although some were taken in the east rookery to avoid interfering with on-going studies. Measurements of elevation, slope (degrees) and distances to the nearest landing beach (measured from the center of colonies) were obtained after mapping the colonies on a detailed topographical map of the west rookery. The number of obstacles (rocks and whale bones) large enough to act as windbreaks (higher than 25 cm) were counted in the west rookery. The distances between the outer rim of a sample of 40 penguin nests and the outer rim of the 3 nearest nests were measured in the east rookery. The length, width and volume (displacement of water) of 5 stones selected at random from a sample of nests from 13, 6 and 25 different Adélie, Chinstrap and Gentoo penguin colonies, respectively (one-third or more of the colonies of each species) were measured in both rookeries. Whenever possible, nest-stone samples were collected from areas in which the 3 species nested in close proximity.

For comparisons, measurement of elevation, slope and the number of obstacles/colony were weighted by multiplying each colony's value by the number of pairs in the colony. All statistical comparisons, unless otherwise indicated, were performed using a 1-way analysis of variance and the Duncan's new multiple range test.

RESULTS AND DISCUSSION

The west rookery consisted of 20 Adélie, 9 Chinstrap and 28 Gentoo penguin colonies (Fig. 1), and a population of 11,000 Adélie, 750 Chinstrap and 700 Gentoo penguin pairs. The east rookery consisted of 22 Adélie, 4 Chinstrap and 55 Gentoo penguin colonies, and a population of 7000 Adélie, 290 Chinstrap and 1900 Gentoo penguin pairs. In the 2 rookeries, the number of pairs per Adélie colony was statistically greater than the number of pairs in Chinstrap and Gentoo penguin colonies, which were statistically equal (Table 1). In the west rookery Adélies nested at higher elevations than chinstraps which nested at higher elevations than gentoos (Table 2). The greatest differences in elevation of nest-sites were evident between Adélies and gentoos. The majority of Adélies nested more than 20 m above sea level, while the majority of gentoos selected nest-sites at less than 10 m elevation. The distance that Adélies nested from the nearest landing beach was statistically greater than the distances chinstraps and gentoos nested from the nearest landing beaches (Table 1). Chinstraps nested in areas of greater slope than gentoos (Table 1). The mean number of obstacles/colony was greater in gentoo colonies than in chinstrap colonies, which had more obstacles than Adélie colonies (Table 1). Adélies nested more closely together than chinstraps which nested more closely together than gentoos (Table 1). The volume of stones used by chinstraps to build nests was statistically greater than those used by Adélies and gentoos (Table 3).

Several differences were apparent among the nest-site characteristics of penguins at Point Thomas. The Adélie Penguin nested in larger, denser colonies which contained fewer obstacles, were at higher elevations and were farther from landing beaches than those of its congeners. The Chinstrap Penguin tended to nest in steeply sloped areas, whereas its congeners nested in generally flat or gently sloped areas, and chinstraps built nests with larger stones than Adélies and gentoos. On Signy Island, Adélie, Chinstrap and Gentoo Penguins are "crest," "slope" and "ridge" nesters, respectively (White and Conroy 1975). In the area of the Antarctic Peninsula, Adélie Penguins nested on knolls and ridges, chinstraps on rocky slopes at higher elevations, and gentoos in low flat areas (Muller-Schwarze and Muller-Schwarze 1975). With the exception of the fact that White and Conroy (1975) reported gentoos at Signy Island nesting primarily on ridges, our findings concur with these.

Chinstraps, in addition to using larger nest-stones than Adélies and gentoos, build their nests with fewer stones than gentoos (Bagshawe 1938). Stones are abundant at Point Thomas, and competition for them is probably nonexistent. Nests built of relatively larger and fewer stones may be an adaptation to nesting in steeply sloped areas where larger stones would provide a more stable anchorage for the nest cup.

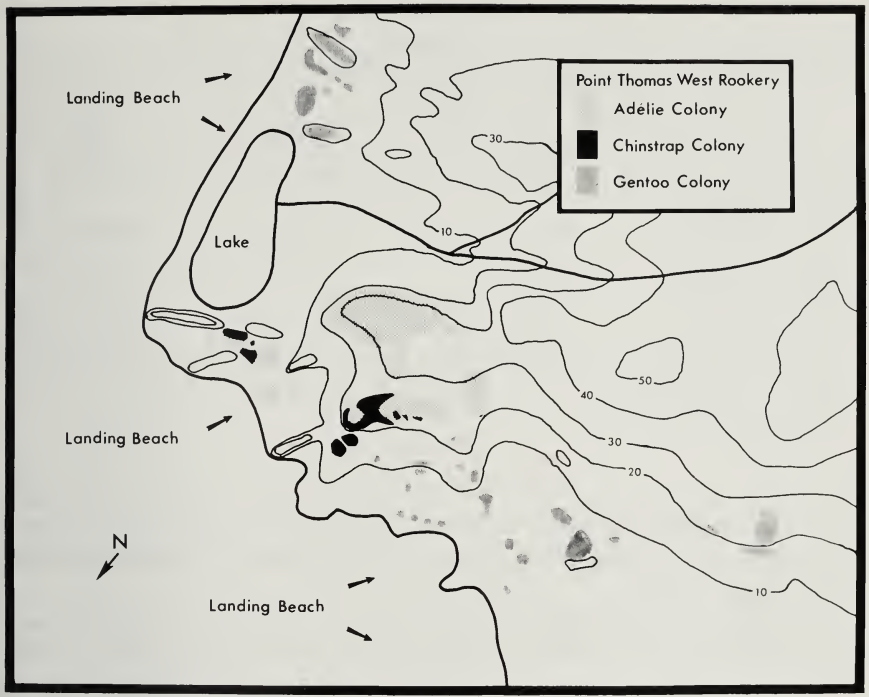


FIG. 1. Map of the Point Thomas west rookery showing the positions of pygoscelid colonies with respect to landing beaches and elevation.

As ice- and snow-free areas suitable for nesting are limited, the nest-site preferences of pygoscelid penguins described in this and other studies may be the result of competition and resource partitioning. Alternatively, we suggest that these preferences may result from differences in their ecology, especially in the degree of coloniality evident in each species. In terms of colony size and nest density, Adélies are the most colonial and gentoos the least colonial. The formation of relatively larger colonies by Adélies requires relatively larger areas, free of obstacles. At Point Thomas these areas are either flat or gentle slopes. In contrast, chinstraps and gentoos, which are less colonial, can exploit nesting habitat which is more broken up, i.e., has more obstacles, is steeper, or is flat, but can accommodate only a few nests, i.e., ridges. The Adélie Penguin, the only pygoscelid which breeds in high latitude rookeries (e.g., Cape Crozier and Cape Royds, Ross Island), nests there on open, wind-swept knoll and ridge tops in order to avoid drifting snow (Yeates 1975). The majority of Adélies at Point Thomas do not nest on knoll and ridge tops, and drifting snow (possibly because of warmer temperatures) does not appear to affect

Table 1

Characteristics ($\bar{x}$ ± SE) of Pygoscelid Penguin Colonies at Point Thomas

	Adélie Penguins	Chinstrap Penguins	Gentoo Penguins
Number of pairs	416.5[a,b**] ± 131.7	81.5 ± 18.7	35.5 ± 4.9
Distance to nearest landing beach (m)	131[a,b*] ± 4.3	93 ± 1.1	92 ± 3.3
Slope (degrees)	5.7 ± 0.4	9.3[a,c**] ± 0.2	4.0[c**] ± 0.2
Number of obstacles per nesting pair	0.09 ± 0.06	0.22 ± 0.04	0.39[a,c**] ± 0.04
Internest distances (cm)	43.2 ± 1.3	59.9[c**] ± 2.2	74.3[a,c**] ± 3.8

[a] Differs statistically from chinstrap.
[b] Differs statistically from gentoo.
[c] Differs statistically from Adélie.
* $P < 0.05$.
** $P < 0.01$.

their reproductive success (Trivelpiece and Volkman, unpubl.), and thus, is probably not as important a factor in their choice of nest-sites here as it is at higher latitudes.

Among the possible adaptive advantages of coloniality to penguins are: (1) protection from predation, (2) protection from adverse weather conditions, (3) social facilitation (i.e., colonies as "information centers," [Ward and Zahavi 1973]), (4) "social stimulation" (after Darling 1938), and (5) maximal exploitation of limited ice- and snow-free areas. At present, data to refute or substantiate any of these possibilities are limited. However, based on available data, a preliminary analysis suggests that none of the first 4 possibilities explains the differing degrees of coloniality among the

Table 2

Percentages of Pygoscelid Penguins Nesting at Different Elevations in the Point Thomas West Rookery

	Elevation (m)			
Species	1–10	11–20	21–30	31–40
Adélie**				
N = 20	13.8	1.2	40.0	45.0
Chinstrap**				
N = 9	17.0	15.2	67.8	0.0
Gentoo**				
N = 28	66.5	22.6	10.9	0.0

** χ^2 significantly different from either congener ($P < 0.01$).

TABLE 3

THE MEAN (± SE) LENGTH, WIDTH AND VOLUME OF NEST-STONES USED BY PYGOSCELID PENGUINS

Species	Length (mm)	Width (mm)	Volume (ml)
Adélie			
N = 45 nests	41.1 ± 1.4	11.1 ± 0.4	6.2 ± 0.4
Chinstrap			
N = 50 nests	52.1 ± 1.5**	11.5 ± 0.6	11.4 ± 0.9**
Gentoo			
N = 54 nests	35.0 ± 1.2	10.6 ± 0.5	5.2 ± 0.5

** Significantly different from Adélie and gentoo ($P < 0.01$).

pygoscelid penguins. The Adélie Penguin does nest farther south than its congeners (see Watson 1975) and there is a correlation between coloniality and latitudinal distribution. Assuming that the amount of ice- and snow-free habitat decreases with increasing latitude, coloniality in pygoscelids may be related to exploitation of ice-free habitat. This conclusion is, of course, preliminary and further data on the ecology of pygoscelid penguins are necessary to substantiate its validity.

SUMMARY

The nest-site preferences of sympatrically breeding Adélie (*Pygoscelis adeliae*), Chinstrap (*P. antarctica*) and Gentoo (*P. papua*) penguins were quantified in rookeries at Point Thomas, South Shetland Islands. Adélies nested in larger, denser, more open colonies, at higher elevations and farther from landing beaches than those of its congeners. Chinstraps nested in steeply sloped areas; Adélies and gentoos nested generally in flat and gently sloped areas. It is suggested that differences in pygoscelid nest-site preferences may be partially attributable to differences in the degree of coloniality evident in each species.

ACKNOWLEDGMENTS

The Polish Academy of Sciences provided logistical and technical support during the austral summer of 1977/1978 at Arctowski Station where the authors were visiting scientists. We thank the personnel of Arctowski, particularly J. Jersak and M. Zalewski, station leaders, for their generous assistance. L. Dutkiewicz, Geographic Institute, Lodz University, kindly provided the topographical map of the west rookery. We thank him for his time, patience and companionship.

Further logistical support was provided by the U.S. Antarctic Research Program and crew of the R/V Hero under the command of Captain P. Lenie. We thank H. Church for photographic asistance and A. Frost for computer facilities. D. Ainley, R. Butler and an anonymous reviewer provided helpful criticisms of this manuscript. This research was supported by grant 75-15506 from the Division of Polar Programs, National Science Foundation, to D. Muller-Schwarze.

LITERATURE CITED

Bagshawe, T. W. 1938. Notes on the habits of the Gentoo and Ringed or Antarctic penguins. Trans. Zool. Soc. Lond. 24:185–306.

Clarke, W. E. 1906. Ornithological results of the Scottish National Antarctic Expedition. II. On the birds of the South Orkney Islands. Ibis ser. 8(6):145–187.

Conroy, J. W. H., O. H. S. Darling and H. G. Smith. 1975. The annual cycle of the Chinstrap Penguin (*Pygoscelis antarctica*) on Signy Island, South Orkney Islands. Pp. 353–363 *in* The biology of penguins (B. Stonehouse, ed.). University Park Press, London, England.

Darling, F. F. 1938. Bird flocks and the breeding cycle: a contribution to the study of avian sociality. The University Press, Cambridge, England .

Klopfer, P. H. and J. P. Hailman. 1965. Habitat selection in birds. Pp. 279–303 *in* Advances in the study of behaviour, Vol. 1 (D. S. Lehrman, R. A. Hinde and E. Shaw, eds.). Academic Press, New York, New York.

Muller-Schwarze, C. and D. Muller-Schwarze. 1975. A survey of twenty-four rookeries of pygoscelid penguins in the Antarctic Peninsula region. Pp. 309–320 *in* The biology of penguins (B. Stonehouse, ed.). University Park Press, London, England.

Murphy, R. C. 1936. Oceanic birds of South America, Vol. 1. Am. Mus. Nat. Hist., New York, New York.

Penney, R. L. 1968. Territorial and social behavior in the Adélie Penguin. Pp. 83–131 *in* Antarctic bird studies. Antarctic Res. Ser., Vol. 12 (O. L. Austin, Jr., ed.). Am. Geophys. Union, Washington, D.C.

Trivelpiece, W. and N. J. Volkman. 1979. Nest-site competition between Adélie and Chinstrap penguins: an ecological interpretation. Auk 96:675–681.

Ward, R. and A. Zahavi. 1973. The importance of certain assemblages of birds as "information centres" for food finding. Ibis 115:517–534.

Watson, G. E. 1975. Birds of the Antarctic and Sub-Antarctic. Am. Geophys. Union, Washington, D.C.

White, M. G. and J. W. H. Conroy. 1975. Aspects of competition between pygoscelid penguins at Signy Island, South Orkney Islands. Ibis 117:371–373.

Yeates, G. W. 1975. Microclimate, climate and breeding success in Antarctic penguins. Pp. 397–409 *in* The biology of penguins (B. Stonehouse, ed.). University Park Press, London, England.

State Univ. New York, Coll. Environmental Sciences and Forestry, Syracuse, New York 13210. (present addresses: Box 1507, Sedona, Arizona 86336 [NJV]; Point Reyes Bird Observatory, 4990 Shoreline Highway, Stinson Beach, California 94970 [WT].)
accepted 23 July 1980.

Wilson Bull., 93(2), 1981, pp. 249–258

COWBIRD PARASITISM AND EVOLUTION OF ANTI-PARASITE STRATEGIES IN THE YELLOW WARBLER

Karen L. Clark and Raleigh J. Robertson

The Yellow Warbler (*Dendroica petechia*) is frequently parasitized by the Brown-headed Cowbird (*Molothrus ater*) resulting in reduction of nest success at parasitized nests (Schrantz 1943, McGeen 1972). There are several avenues open to a Yellow Warbler once a cowbird egg has been deposited in its nest. It could accept the egg, thereby running the risk of the egg hatching and the cowbird nestlings competing with the Yellow Warbler nestlings. Alternatively, it could reject the egg. This could occur by ejection, where the cowbird egg is removed from the nest (cf. Rothstein 1975), by nest desertion, or by burial, in which the cowbird egg, along with any Yellow Warbler eggs present at the time, are covered by the addition of nesting material. The response favored by natural selection depends upon the potential for a successful nest attempt. The possibility of success varies with the amount of time and energy already invested in the nesting attempt, and the possibility of the cowbird egg hatching. The objectives of this study were to determine the frequency of occurrence of these various responses by Yellow Warblers to naturally deposited cowbird eggs and to investigate the factors eliciting each response.

METHODS

Yellow Warbler nests were located in several study areas near the Queen's University Biological Station, Chaffey's Locks, Ontario, from 1975–1977. Most nests were found during nest building. Nests for which the date of clutch initiation was unknown have not been included in this analysis unless noted. In 1975 and 1976, nests were checked every second day. In 1977, nests were checked daily during egg-laying and early incubation and then every third day until the young fledged. All references to number of Yellow Warbler eggs indicate the number present when the nest was checked. In some parasitized nests, 1 or more Yellow Warbler eggs may have been removed by cowbirds. Our measure of nest success was the number of young leaving the nest as a proportion of the number of eggs laid. All references to nest success are only to those nests not preyed upon. For nests which received more than 1 cowbird egg, only the response to the first egg is included in tables and text unless specified otherwise.

RESULTS AND DISCUSSION

Forty-one percent (45/109) of all Yellow Warbler nests were parasitized, containing 1 or more cowbird eggs (Table 1). The mean nest success of parasitized nests was 0.44 ± 0.33 compared to the mean nest success of unparasitized nests of 0.80 ± 0.16 (Mann Whitney *U*-test, *U* for large

Table 1

Mean Nest Success of Parasitized and Unparasitized Nests

Nest status	No. Yellow Warbler nests	No. cowbird eggs	$\bar{x}$ ± SD Nest success[a] (no. of nests)
Parasitized			
Buried	20[b]	28	0.78 ± 0.21 (13)
Deserted	10	12	0.0 ± 0.0 (10)
Accepted	12	16	0.53 ± 0.34 (8)
Preyed upon[c]	3	3	(0)
Total	45	59	0.44 ± 0.33 (31)
Not parasitized	64	0	0.80 ± 0.16 (35)

[a] Nest success = Yellow Warbler young to leave the nest per egg laid, including buried eggs, based only on nests (number as indicated) which were not preyed upon prior to fledging.

[b] Two nests are included which were found after clutch initiation and are not included in subsequent tables.

[c] Number of nests preyed upon before the response to the cowbird egg could be determined. They are included here to indicate the incidence of parasitism. These nests are not included in subsequent tables or in percent frequency of responses cited in text.

samples = 3.01, $P \leq 0.01$). The number of nestlings lost per nest varied greatly from 0 to some (variable) threshold number leading to termination of the nesting attempt. The reduction in nest success depended on the number of Yellow Warbler eggs removed by the cowbird, the stage of nesting when the cowbird egg was laid, and the response of the Yellow Warbler to the cowbird egg (Table 2). For 8 of 9 nests which received more than 1 cowbird egg the response to subsequent eggs was the same as for

Table 2

Acceptance and Rejection of Cowbird Eggs as a Function of the Number of Yellow Warbler Eggs When the Cowbird Egg was Deposited

No. YW eggs[a]	No. YW nests	No. CB eggs[b]	No. nests with cowbird eggs			$\bar{x}$ (± SD) nest success[c]	
			buried	de-serted	ac-cepted	YW	CB
0	20	30	13	7	0	0.52 ± 0.42	0.0 ± 0.0
1	4	4	3	0	1	0.48 ± 0.21	0.0 ± 0.0
2	6	6	1	1	4	0.31 ± 0.52	0.17 ± 0.41
3	4	7	0	2	2	0.30 ± 0.48	0.67 ± 0.58
4	5	5	1	0	4	0.50 ± 0.25	0.20 ± 0.45
5	1	1	0	0	1	—	—

[a] Number of Yellow Warbler eggs present when the cowbird egg was laid. In some cases, a Yellow Warbler egg may have been removed by the cowbird.

[b] Total number of cowbird eggs laid, not per nest. Most nests contained only 1 cowbird egg, although some contained more than one.

[c] Nest success measured as the number of young to leave nest/eggs laid/nest, excluding nests that were preyed upon.

the first. At 1 nest the first cowbird egg was laid before any Yellow Warbler eggs, and it was buried. A second egg laid when there were 3 Yellow Warbler eggs resulted in desertion of the nest.

Acceptance of cowbird eggs.—Cowbird eggs were accepted at only 29% (12/42) of all parasitized Yellow Warbler nests (Table 1). The mean nest success of Yellow Warblers which accepted cowbird eggs was 0.53 ± 0.34 (Table 1) and where cowbird young fledged was 0.46 ± 0.33 (N = 6). Acceptance occurred most frequently at nests which had 2 or more Yellow Warbler eggs at the time the cowbird egg was laid (Tables 2, 3). These results are similar to those of Rothstein (1975) who found 100% acceptance at 16 Yellow Warbler nests which were experimentally parasitized when they contained at least 2 warbler eggs. Accepted cowbird eggs that were laid when there were 3 Yellow Warbler eggs in the nest had the highest success, although the small sample size of cowbird eggs accepted when there were 0, 1 or 5 Yellow Warbler eggs was insufficient to assess cowbird success in these nests.

The cowbird incubation period is 10–11 days (Friedmann 1963) whereas the Yellow Warbler's is 11–12 days (Schrantz 1943, this study). Yellow Warblers will initiate incubation before their clutch is complete. With a mean clutch-size of 3.6 ± 0.82 eggs for parasitized Yellow Warblers, cowbird eggs deposited on or before the day the third egg was laid hatch with or before the Yellow Warbler eggs. The chance of hatching for a cowbird egg laid when there were 3 or fewer Yellow Warbler eggs in the nest was 83% (5/6, including only nests with accepted cowbird eggs which were not preyed upon). In 3 of these 5 nests where the cowbird egg did hatch, only 1 Yellow Warbler fledged along with the cowbird. In each of the three, the cowbird hatched earlier than any of the Yellow Warblers. In the other 2 nests, in which the cowbirds hatched synchronously with or later in the day than the warblers, 3 and 4 Yellow Warblers, respectively, fledged along with the parasite's young. The time of hatching of Yellow Warbler eggs relative to cowbird eggs thus appears to be a key determinant of Yellow Warbler hatching success and nestling survival. Mayfield (1960: 173) found that Kirtland's Warbler (*Dendroica kirtlandii*) nestlings never survived when there were 2 or more older cowbird nestlings in the nest, and survival was greatly reduced when there was 1 older cowbird nestling. However, Kirtland's Warblers which hatched 2 or more days before the cowbird egg hatched were not adversely affected by the presence of the cowbird.

Another factor predicted to influence the response of the Yellow Warbler to parasitism is the timing of the event with respect to the breeding season. A delay due to egg burial or renesting could have detrimental effects associated with the timing of the nest, relative to the rest of the

Table 3

Frequency of Occurrence of Rejection and Acceptance of Cowbird Eggs Relative to Yellow Warbler Nest Stage

No. YW eggs when CB egg was laid	No. YW nests	Frequency of response % (no.) of nests where cowbird eggs were[a]		
		buried	deserted	accepted
0, 1	24	67 (16)[b]	29 (7)[c]	4 (1)[d]
2–5	16	12 (2)[b]	19 (3)[c]	69 (11)[d]

[a] $\chi^2 = 20.02$, df = 2, $P < 0.001$—indicating that the 3 responses occurred with different frequency within host egg number groupings.

[b] $\chi^2 = 11.38$, df = 1, $P < 0.001$—indicating that the frequency of burial is different for clutches of 0–1 vs 2–5, when other responses are grouped.

[c] $\chi^2 = 0.55$, df = 1, $P > 0.05$—indicating that the frequency of desertion is similar regardless of number of host eggs when nest is parasitized.

[d] $\chi^2 = 19.07$, df = 1, $P < 0.001$—indicating that the frequency of acceptance is different for clutches of 0–1 vs 2–5, when other responses are grouped.

avian community. Asynchronous Yellow Warbler nests were subjected to higher predator pressure than nests in synchrony with the community as a whole (Clark and Robertson 1979), a difference possibly attributable to either the "swamping effect" or "selfish herd effect" on predators (Robertson 1973, Hamilton 1971). Furthermore, since a bird's initial nesting attempt is thought to be timed to take advantage of optimal conditions, delay could put the Yellow Warbler nest out of phase with the food supply (Immelmann 1971). Late in the nesting season the risk of loss associated with a delay could outweigh the potential benefits of cowbird egg rejection. Consequently, acceptance, which minimizes any delay in nesting, is expected to occur more frequently later in the breeding season.

Since response was shown to depend on the stage of the nest at the time of parasitism (Table 3) this factor should be considered when investigating seasonal changes in response. Rearranging the data into the many small categories necessary for such an analysis produced sample sizes inadequate for statistical analysis. It was evident, however, that there was a relationship between date and stage of the nest when parasitized. Defining the peak of clutch initiation as the day on which the maximum number of Yellow Warbler clutches were initiated, we found that parasitism of nests containing 0 or 1 Yellow Warbler egg(s) occurred most frequently before this peak (18 of 24 nests containing 0 or 1 Yellow Warbler egg(s) were parasitized before the peak of clutch initiation). Nests with 2 or more Yellow Warbler eggs were less frequently parasitized before the peak of clutch initiation (where 4 of 18 nests with 2 or more Yellow Warbler eggs were parasitized before the peak in clutch initiation, $\chi^2 = 11.49$, df = 1, $P < 0.01$). Because of this association between the

TABLE 4

FREQUENCY OF OCCURRENCE OF REJECTION AND ACCEPTANCE OF COWBIRD EGGS IN YELLOW WARBLER NESTS DURING THE BREEDING SEASON

Breeding season when YW nest parasitized	No. YW nests	Frequency of response % (no.) of nests where cowbird eggs were[a]		
		accepted	deserted	buried
Before peak of Yellow Warbler clutch initiation[b]	22	68 (15)[c]	23 (5)[d]	9 (2)[e]
After peak of Yellow Warbler clutch initiation	18	17 (3)[c]	28 (5)[d]	56 (5)[e]

[a] $\chi^2 = 13.06$, df = 2, $P < 0.002$—indicating that the 3 responses occurred with different frequency within season categories.

[b] Peak of clutch initiation defined as the day when the maximum number of Yellow Warbler clutches were initiated: 22 May 1975, 29 May 1976 and 26 May 1977.

[c] $\chi^2 = 10.18$, df = 2, $P < 0.002$—indicating that acceptance occurred with different frequency before vs after peak, when other responses are grouped.

[d] $\chi^2 = 0.13$, df = 1, $P > 0.05$—indicating that desertion rate was similar before and after peak.

[e] $\chi^2 = 10.61$, df = 1, $P < 0.001$—indicating that burial occurred with different frequency before vs after peak, when other responses are grouped.

number of host eggs present when the nest was parasitized and date, it is apparent that the different responses to cowbird eggs may have resulted from either nest stage or date, or a combination of both; although acceptance did occur more frequently after the peak of clutch initiation (Table 4), this is also when nests with 2 or more Yellow Warbler eggs were more frequently parasitized. Thus, it is not possible to decide which factor was more influential in determining the response. Interestingly, the only nest in which acceptance occurred when there were 0 or 1 Yellow Warbler egg(s) present was parasitized after the peak of clutch initiation.

Cowbird egg rejection by ejection.—No instances of egg ejection by the Yellow Warbler were recorded. Rothstein (1975) has shown that the Yellow Warbler beak-length-to-parasite-egg-width ratio is larger than the same ratio for some other species, suggesting that Yellow Warblers are capable of ejecting cowbird eggs. However, Rothstein (1976) also found that the Cedar Waxwing (*Bombycilla cedrorum*) has problems ejecting eggs, often incurring nest damage and/or bruising in the process. He attributed this to the small bill size of the Cedar Waxwing. Yet this species has a beak-length-to-ejected-egg-width ratio well above that of the Yellow Warbler, which has the smaller exposed culmen (9.1 mm vs 10.1 mm) of the two (Godfrey 1966). The Yellow Warbler is also smaller in body size, with a range of weight of 9.3–12.3 g (Raveling and Warner 1978) compared to the Cedar Waxwing which has a weight in the range of 30–42.5 g (Roberts

1955). If the Cedar Waxwing has problems ejecting cowbird eggs the smaller Yellow Warbler would likely have even greater difficulty in this regard.

Possibly a Yellow Warbler incapable of ejecting an intact cowbird egg might first break the egg and then remove it. However, piercing and/or breaking up an egg would likely be disadvantageous, as spilling the contents on the other eggs in the nest could make them difficult to roll during incubation (Rothstein 1975). In addition, the nest might be more vulnerable to ant infestations.

Egg rejection by burial.—Egg burial was the Yellow Warbler's most common response to a cowbird egg and occurred at 20 of 42 (48%) parasitized nests (Table 1). Burial occurred most frequently when 0 or 1 Yellow Warbler egg(s) were in the nest (Table 3). Egg burial requires a small energy expenditure on the part of the Yellow Warbler in building a new floor and increasing the sides of the nest. It also allows the bird to lay a new clutch, thus eliminating the threat of the cowbird egg hatching and a reduction in clutch-size due to the cowbird's removing a host egg. The mean clutch-size (excluding buried eggs) of Yellow Warbler nests with buried cowbird eggs (4.1 ± 0.92) was the same as at nests which were not parasitized (4.1 ± 0.55 eggs), suggesting that females were physiologically capable of producing replacement eggs to compensate for those buried. The 0.5 egg difference between the unparasitized clutch-size of mean 4.1 and the parasitized clutch-size of mean 3.6 suggests that, on average, the cowbird removes a host egg from 1 out of 2 nests it parasitizes.

The delay in nesting caused by egg burial depended upon the number of Yellow Warbler eggs that were buried along with the cowbird eggs, since these would have to be replaced in the new clutch. The mean time delay to initiation of a new clutch was 3.1 ± 1.6 days. When the cowbird egg was laid in a nest which was not complete the delay was shorter, since it could be almost entirely buried by a thick layer of lining. For each Yellow Warbler egg that was buried the delay was increased by 1 day. The energy loss from the investment in the buried eggs would also increase with each buried egg. Perhaps because of the large energy losses and extended time delays cowbird eggs were seldom buried along with more than 1 Yellow Warbler egg.

Rothstein (1975) has suggested that the Yellow Warbler's choice of nest material may be an anti-parasite adaptation. In his study, the lining of the nests was very similar to the material used in the nest frame so cowbirds may have been unable to determine when the nest was complete. The cowbird might then lay before completion, and its egg could be buried while the Yellow Warbler was finishing the nest. Mayfield (1960:156) noted that in some Kirtland's Warbler nests the cowbird eggs laid before the nest was completed were occasionally buried in the lining. The Yellow

Warbler nests in our study tended to be lined with a material distinctive from that used in the nest frame. The lining was usually a fluffy plant down, while the frame was usually coarse plant fibers. Although cowbirds may have mistaken some nests as complete when laying, other times cowbird eggs were laid when the floor of the frame was obviously incomplete. McGeen (1972) noted that the cowbird has difficulty timing its egg-laying with the nesting of the Yellow Warbler, especially when there are Song Sparrows (*Melospiza melodia*) nesting in the vicinity. Song Sparrows are a better host for the cowbird than the Yellow Warbler, and cowbird egg-laying is usually synchronized with the first nesting of the Song Sparrow, which is earlier than that of the Yellow Warbler. Synchronization of the egg-laying period by cowbirds in our study areas with that of Song Sparrows (which were common in the area) might account for the laying of cowbird eggs in unfinished Yellow Warbler nests.

The occurrence of egg burial at 5 nests where Yellow Warbler eggs were buried along with a cowbird egg indicates that egg burial was not always a result of overlap between cowbird laying and Yellow Warbler nest building. In these 5 nests, egg burial must have been a direct response to the cowbird egg.

Egg burial occurred most commonly before the peak of clutch initiation, when a delay would not place the nest greatly out of synchrony with the rest of the avian community (Table 4). An extremely late nesting Yellow Warbler would be susceptible to the disadvantages of asynchronous nesting described earlier.

Yellow Warbler nests which had a cowbird egg buried were no more susceptible to being parasitized again. Of 20 nests which had a cowbird egg buried only two were parasitized again compared to the incidence of parasitism at other nests where 25 out of 89 were parasitized ($\chi^2 = 2.87$, df = 1, $P > 0.10$, NS). Egg burial resulted in a mean nest success of 0.78 ± 0.21, which was not significantly different from 0.80 ± 0.16, the mean success of unparasitized nests (Table 1; Mann-Whitney *U*-test, *U* for large samples = 0.85, $P > 0.05$). The significantly lower nest success of acceptor nests (0.53 ± 0.34) compared to nests where cowbird eggs were buried (0.78 ± 0.21) (Mann-Whitney *U*-test, $U = 47$, $P < 0.05$) suggests that egg burial may be an adaptive response to cowbird parasitism.

Egg rejection by nest desertion.—Nest desertion occurred at 24% (10/42) of the parasitized nests, most commonly when 0 or 1 Yellow Warbler egg(s) were in the nest (assuming that in at least some cases, the cowbird removed a Yellow Warbler egg) (Table 2). The advantages of nest desertion were impossible to assess as the success of a second nesting attempt could not be determined without individually marked birds. Also, this estimate of desertion rate is likely conservative since deserted nests are more difficult

to find. Nests deserted early involved minimal time and energy investment and the potential for successful renesting would have been high. In contrast, pairs of Yellow Warblers deserting nearly complete clutches would have incurred a delay of 6–9 days (2–4 days to build a nest and 4–5 days to lay a new clutch). The nesting season of the Yellow Warbler is sufficiently short (they are normally single brooded at this latitude) that the potential for renesting after a delay of this length is much reduced. Selection may thus favor burial over desertion early in the season because of the shorter time delay and lower energy costs. In the case of the pair which buried 1 cowbird egg but deserted after a second was laid, it may be that building a second floor and replacing the buried 3-egg clutch resulted in a delay that made desertion the best strategy.

Desertions occurred with the same frequency before and after the peak of clutch initiation. One explanation for desertion regardless of the time in the nesting season would be that in some cases the nest support structure was inadequate to allow a new floor to be built for egg burial. In fact, we observed 1 nest where the floor had been initiated over a cowbird egg, but before it was complete the nest became unstable. This nest was then deserted and a new nest was initiated less than 1 m away. Nest desertion may have also occurred late in the season as an alternative means of rejection when egg burial would have resulted in a deleterious time delay. Selection may act to favor desertion and termination of the nesting if the potential for Yellow Warbler success is low and if desertion would increase fitness in the following breeding season. High adult mortality during migration may seriously weaken evidence supporting this last hypothesis.

It is difficult to determine whether nest desertion occurred in response to a cowbird egg, human observer disturbance at nests, altered clutch-size or the discovery of the cowbird at the nest (Rothstein 1976). In this study, desertions occurred at 24% (10/42) of parasitized nests and only 3% (2/64) of unparasitized nests ($\chi^2 = 15.43$, df = 1, $P < 0.001$). Since all nests were checked in a similar fashion the majority of desertions are probably due to cowbird parasitism. Desertion at the 2 unparasitized nests occurred after a single egg had been removed each day until in 1 nest there was 1 egg left and in the other 2 eggs were left. The eggs at these nests may have been removed by either cowbirds or predators. Since there were, however, few predators which take eggs in this fashion in our study area, desertion in these cases may also have been due to cowbirds.

Cowbirds would frequently remove a host egg before laying their own so that clutch-size was not increased in parasitized nests. Yellow Warblers occasionally had clutches of 5 eggs, which were successful; the total number of eggs in a parasitized nest exceeded 5 in only 1 nest. The cowbird and 2 of the Yellow Warbler eggs in the clutch eventually hatched. Thus,

an inhibition of incubation behavior by the alteration of clutch-size does not likely account for the desertion of parasitized nests.

Desertion occurred most frequently when there were no Yellow Warbler eggs in the nest. The appearance of a cowbird egg before the Yellow Warbler had initiated her own clutch, or the replacement of the first warbler egg with a cowbird egg on the day of initiation, may have been the main cause of nest desertion. Desertion may thus be an anti-parasite strategy evoked in direct response to the appearance of cowbird eggs. Alternatively, desertion may be a response to foreign objects in the nest (Rothstein 1975). Discovery of the cowbird at the nest may also have resulted in a sufficient disturbance to cause desertion in some instances. Since birds will often desert if disturbed by a predator, the presence of a cowbird might provide a similar stimulus to desert. However, Robertson and Norman (1976, 1977) showed that aggressive responses to cowbirds can reduce the incidence of parasitism, so one might expect that a fleeing response of hosts should be selected against. Also, cowbirds which harass their hosts to the extent of causing nest desertion would be selected against, since they would be lowering the number of available host nests and reducing the success of their own eggs. Thus, it seems most likely that some Yellow Warblers desert nests due to the presence of the cowbird egg per se.

In conclusion, the Yellow Warbler appears to have evolved a finely tuned anti-parasite strategy involving the rejection of cowbird eggs by either egg burial or nest desertion dependent upon the stage of the nest in which the cowbird egg is deposited and upon the timing of the nest with respect to its neighbors. This strategy reduced both the success of cowbird eggs in Yellow Warbler nests and Yellow Warbler losses due to parasitism.

SUMMARY

We recorded the responses of nesting Yellow Warblers to naturally deposited Brown-headed Cowbird eggs. The response varied, depending upon the stage of the nest when the cowbird egg was deposited, the time of the breeding season and the structure of nest support. An association between nest stage and time in the breeding season did not allow any conclusions about the relationships between either of these factors and response to the cowbird egg to be made, although both were thought to be influencing the choice of response. Acceptance of cowbird eggs resulted in significantly lower nest success for Yellow Warblers. The most frequent rejection response by the Yellow Warbler was burial of cowbird eggs. Parasitized nests in which burial occurred had success rates comparable to unparasitized nests. Egg burial was used as an anti-parasite strategy primarily when the cowbird egg was deposited early in the Yellow Warbler's laying cycle. Nest desertion was the alternative rejection response. Desertion, which released the pair from a nesting attempt in which the potential for success was low, occurred throughout the breeding season. Desertion was thought to occur when egg burial was not possible, either because of the resulting delay, or when the nest support structure would not allow burial.

ACKNOWLEDGMENTS

This study benefited greatly from the use of the Queen's University Biological Station. Dave Cameron, Richard Norman and Patrick Weatherhead assisted with the nest records and Patrick Colgan helped with the statistics. This paper was greatly improved by the reviews of S. I. Rothstein and A. L. A. Middleton and the editorial assistance of N. Flood. These contributions and research support to Raleigh J. Robertson from Queen's University and the National Research Council of Canada are gratefully acknowledged.

LITERATURE CITED

Clark, K. L. and R. J. Robertson. 1979. Spatial and temporal multi-species nesting aggregations in birds as anti-parasite and anti-predator strategies. Behav. Ecol. Sociobiol. 5:359–371.

Friedmann, H. 1963. Host relations of the parasitic cowbirds. Smithson. Inst. Washington, D.C.

Godfrey, W. E. 1966. The birds of Canada. Natl. Mus. Canada Bull. No. 203.

Hamilton, W. D. 1971. Geometry for the selfish herd. J. Theoret. Biol. 31:295–311.

Immelmann, K. 1971. Ecological aspects of periodic reproduction. Pp. 342–489 *in* Avian biology, Vol. 1. D. S. Farner and J. R. Kings, eds. Academic Press, New York, New York.

Mayfield, H. 1960. The Kirtland's Warbler. Cranbrook Inst. Sci., Bloomfield Hills, Michigan.

McGeen, D. S. 1972. Cowbird-host relationships. Auk 89:360–380.

Raveling, D. G. and D. W. Warner. 1978. Geographic variation of Yellow Warblers killed at a TV tower. Auk 95:73–79.

Roberts, T. S. 1955. Manual for the identification of birds of Minnesota and neighboring states. Revised ed. Univ. Minnesota Press, Minneapolis, Minnesota.

Robertson, R. J. 1973. Optimal niche space of the Red-winged Blackbird: spatial and temporal patterns of nesting activity and success. Ecology 54:1085–1093.

——— and R. F. Norman. 1976. Behavioral defenses to brood parasitism by potential hosts of the Brown-headed Cowbird. Condor 78:166–173.

——— and ———. 1977. The function and evolution of aggressive host behavior towards the Brown-headed Cowbird (*Molothrus ater*). Can. J. Zool. 55:508–518.

Rothstein, S. I. 1975. An experimental and teleonomic investigation of avian brood parasitism. Condor 77:250–271.

———. 1976. Experiments on defences Cedar Waxwings use against cowbird parasitism. Auk 93:675–691.

Schrantz, F. C. 1943. Nest life of the eastern Yellow Warbler. Auk 60:367–387.

DEPT. BIOLOGY, QUEEN'S UNIV., KINGSTON, ONTARIO K7L 3N6 CANADA. ACCEPTED 16 JULY 1980.

Wilson Bull., 93(2), 1981, pp. 259–264

INTERACTIVE BEHAVIOR AMONG BALD EAGLES WINTERING IN NORTH-CENTRAL MISSOURI

Curtice R. Griffin

Despite the increasing interest in the Bald Eagle (*Haliaeetus leucocephalus*) attested to by recent field studies (Shea 1973; Lish and Lewis 1975; Servheen 1975; Steenhof 1976; Stalmaster and Newman 1978, 1979), few published reports describe intraspecific behavior of Bald Eagles in winter. The present paper describes the frequency and extent of intraspecific conflict, and discusses the possible consequences of patterns of interactions between adults and immatures.

Eagles commonly displace one another from food items and perches (Southern 1963, Shea 1973, Servheen 1975). Intraspecific aggression may be most common during feeding periods (Jonen 1973), and adults usually dominate immature birds in aggressive encounters (Erskine 1968). In Oklahoma, Lish (1973) described displacement, tail chasing (aerial pursuit) and talon presentation behavior of wintering Bald Eagles. From these observations, Lish suggested that a social hierarchy might exist on the wintering grounds. Stalmaster and Newman (1979) stated that the oldest bird usually occupied the highest site when eagles of different age classes perched in the same tree.

METHODS

I watched the behavior of Bald Eagles almost daily from October 1975–March 1976 at Swan Lake National Wildlife Refuge, Chariton Co., north-central Missouri. I observed intraspecific behavioral dominance at or near feeding areas and perch sites, but not near night roosts. I used binoculars (7 × 50 mm) and a spotting scope (15–60×), and made all observations from a vehicle or blind. Birds with entirely white heads and tails were classed as adults; all others were classed as immatures.

Types of aggressive encounters included displacement, aerial pursuit and talon presentation. Criteria of dominance in displacement encounters included the supplanting of 1 eagle by another from a food item or perch, or the fleeing of an eagle when another approached. Aerial pursuits involving more than 1 chasing bird were tallied according to age classes of the birds involved. Only 1 talon presentation was tallied per encounter regardless of the number occurring. To compare participation in aggressive encounters by birds of the 2 age classes, it is necessary to take into account the proportion of birds in each age class. Accordingly, these analyses followed Hailman's (1975) procedure, incorporating a Chi-square test. Twenty-two ground counts were made during the study.

RESULTS AND DISCUSSION

Numbers of Bald Eagles on Swan Lake Refuge fluctuated throughout the winter. A peak of 66 birds occurred on 2 December. In 22 censuses, 353 observations of immatures and 248 of adults were recorded. The adult

Table 1

Displacement Attempts, Aerial Pursuits and Talon Presentations of Immature and Adult Bald Eagles, Swan Lake National Wildlife Refuge

Types of encounter	Immature—Immature[a]	Immature—Adult	Adult—Immature	Adult—Adult	Total
Displacement[b]	102[c] (10)	40[c] (3)	32[d] (1)	64[d] (1)	238 (15)
Percent of total	43%	17%	13%	27%	100%
Aerial pursuits	45[d]	9	3[d]	4[d]	61
Percent of total	74%	15%	5%	6%	100%
Talon presentation	23[d]	3	0[c]	1	27
Percent of total	85%	11%	—	4%	100%

[a] Initiator—recipient.
[b] Numbers of unsuccessful displacement attempts in parentheses.
[c] $P < 0.05$, numbers of encounters according to age class differing from expected (see text).
[d] $P < 0.01$, numbers of encounters according to age class differing from expected (see text).

component ranged from 0–$^4/_5$ of the observed winter population. Detailed information on eagle populations at the refuge during this study is in Griffin (1978).

Feeding.—Feeding was highly communal. A few (2–3) to more than 30 eagles fed close together. Eagles rarely shared the same food item. Most of the heavier food items, waterfowl and fish carcasses, were consumed on the ground or ice. Eagles waded to carcasses in shallow water and dragged them to shore or onto a low perch to feed. Eagles sometimes gathered small carcasses from the water, frozen impoundments or shore by swooping upon them without landing.

Displacement.—Bald Eagles were seen attempting to displace each other from food carcasses and perches at the feeding areas 238 times. All but 15 (6.3%) attempts were successful. Of 238 attempts, 102 (43%) were between immature birds and 64 (27%) between adults. Immature eagles attempted to displace adult birds in 40 (17%) of the observations and adult eagles tried to displace immatures in 32 (13%) (Table 1).

Aerial pursuit and talon presentation.—Aerial pursuits and talon presentation (Fig. 1) occurred at both low and high altitudes throughout the winter, whether or not food was being carried. In a pursuit, one or more eagles chased another, sometimes flying within 0.5 m of each other. Eagles used a fast descending glide when chasing and a labored flapping flight when pursuit was intense. The pursued eagle performed evasive maneuvers, usually steep dives or dives followed by a steep climb. Most aerial pursuits lasted less than 30 sec; however, some pursuits lasted at least 8 min, with the birds flying out of sight. Of 61 observations of aerial pursuits, 27 (44%) involved at least 1 talon presentation. In some instances, after presenting talons, the pursued bird became the pursuer.

FIG. 1. Aerial pursuit and talon presentation of Bald Eagles (after Lish 1973).

Talon presentation occurred when one of the pursuing eagles dived at another in flight. As the diving eagle neared the lower-flying eagle, the latter flipped over and presented its talons. Contact between the bodies of the 2 eagles occurred occasionally. This behavior is similar to Bald Eagle courtship displays (Brown and Amadon 1968) except that whirling with the talons locked does not occur.

The interactions of immature and adult eagles during aerial pursuit and talon presenting are tallied in Table 1. Immature eagles pursued and presented talons to adults or other immatures in most observations. Adult eagles pursued immatures or other adults in only 11% of the aerial pursuit observations. There were no observations of adults presenting talons to immatures, and only 1 observation (4%) of an adult presenting talons to another adult.

Some aerial pursuits and talon presentations involved stealing of food in flight. The number of cases was not determined because of the difficulty of seeing food in the talons. In food-stealing encounters, 1–5 eagles approached the food-carrying bird from the rear, pursuing birds flipped over and took the food from the pursued bird's talons or dived repeatedly, forcing the pursued eagle to drop the food. Once food was dropped, a pursuing eagle attempted to recover it.

Patterns of interactions related to age.—Considering their relative abundances, adult eagles initiated significantly fewer displacement attempts

($\chi^2 = 11.427$, df = 1, $P < 0.01$, N = 238), aerial pursuits ($\chi^2 = 9.389$, df = 1, $P < 0.01$, N = 61) and talon presentations ($\chi^2 = 6.540$, df = 1, $P < 0.05$, N = 27) with immatures than expected. However, adult birds attempted to displace other adults more frequently than expected ($\chi^2 = 13.611$, df = 1, $P < 0.01$, N = 238). Immatures often entered into displacement attempts ($\chi^2 = 4.828$, df = 1, $P < 0.05$, N = 238), aerial pursuits ($\chi^2 = 27.285$, df = 1, $P < 0.01$, N = 61) and talon presentation ($\chi^2 = 20.151$, df = 1, $P < 0.01$, N = 27) with other immatures; however, immatures infrequently attempted displacement of adults ($\chi^2 = 5.415$, df = 1, $P < 0.05$, N = 238) (Table 1). These apparent patterns must be viewed with some caution, because the behavior was possibly influenced by severity of weather, abundance of food and numbers of eagles present. These conditions changed frequently and their effects could not be analyzed.

The potential is great for severe injury from aggressive fighting of such a large and pugnacious bird as an adult Bald Eagle, and immature eagles are probably seldom competitive with adults at aggressive fighting. Conditioning from previous encounters probably has encouraged a dominance-subordinance relationship favoring adults as has been indicated for many large aggressive mammals such as lions (*Panthera leo*) (Schaller 1972), wolves (*Canis lupis*) (Mech 1970) and a number of primate species (Brown 1975).

Several studies of avian foraging have shown that the ability to obtain food improves with age (reviewed by Buckley and Buckley 1974, Verbeek 1977). To compensate for lesser prowess at finding, capturing and defending food, immature eagles may be forced to (1) spend more time than adults in searching for food, (2) seek alternative food sources, (3) use different wintering areas than adults, or (4) resort to stealing. The fourth alternative may lead to the strong tendency noted in this study for immature eagles to enter into aggressive encounters at feeding areas. The third alternative may also be important. The age ratio of immatures to adults at the refuge is lowest during the periods of harshest weather and lowest food availability (Griffin 1978). This fact and the known tendency for immature eagles to winter farther south than adults (Sprunt and Cunningham 1962, Ingram 1965, Sprunt and Ligas 1966) indicate than many immature eagles may seek wintering areas not used by adults.

SUMMARY

Wintering Bald Eagles displayed food and perch displacement, aerial pursuit and talon presentation behavior on the wintering grounds. Immature eagles initiated most of these behavioral interactions, and most displacement attempts were successful. In displacement attempts, immatures tried to displace adults somewhat more frequently than adults tried to displace immatures. Nearly half of all aerial pursuits involved at least 1 talon presentation. An undetermined number of aerial pursuits and talon presentations involved food being

stolen from the pursued eagle. Considering their relative abundances, adult eagles initiated significantly fewer displacement attempts, aerial pursuits and talon presentations with immatures than expected. Although immatures often entered into all 3 behavioral interactions with other immatures, they infrequently attempted displacement of adults.

ACKNOWLEDGMENTS

I thank J. R. Acker, B. S. Johnson and M. Murphy for their assistance in the field. I am grateful to F. B. Samson and T. S. Baskett for their critical review of this manuscript. This report is a contribution from the Missouri Cooperative Wildlife Research Unit (School of Forestry, Fisheries and Wildlife, University of Missouri, Missouri Department of Conservation, U.S. Fish and Wildlife Service, and Wildlife Management Institute, cooperating). The work was funded in part by the National Audubon Society and U.S. Fish and Wildlife Service Contract No. USDI 14–16–0008–757, awarded to the University of Missouri.

LITERATURE CITED

Brown, L. and D. Amadon. 1968. Eagles, hawks, and falcons of the world. Vol. 1. McGraw-Hill, New York, New York.

Brown, J. L. 1975. The evolution of behavior. W. W. Norton and Co., New York, New York.

Buckley, F. G. and P. A. Buckley. 1974. Comparative feeding ecology of wintering adult and juvenile Royal Terns. Ecology 55:1053–1063.

Erskine, A. J. 1968. Encounters between Bald Eagles and other birds in winter. Auk 85:681–683.

Griffin, C. R. 1978. The ecology of Bald Eagles wintering at Swan Lake National Wildlife Refuge, with emphasis on eagle-waterfowl relationships. M.S. thesis, Univ. Missouri, Columbia, Missouri.

Hailman, J. P. 1975. Analysis of aggression in White-throated Sparrow types of different proportions. Bird-Banding 46:236–240.

Ingram, T. N. 1965. Wintering Bald Eagles at Guttenberg, Iowa—Cassville, Wisconsin, 1964–1965. Iowa Bird Life 35:66–78.

Jonen, J. R. 1973. The winter ecology of the Bald Eagle in west-central Illinois. M.S. thesis, Western Illinois Univ., Macomb, Illinois.

Lish, J. W. 1973. Status and ecology of Bald Eagles and nesting of Golden Eagles in Oklahoma. M.S. thesis, Oklahoma State Univ., Stillwater, Oklahoma.

——— and J. C. Lewis. 1975. Status and ecology of Bald Eagles wintering in Oklahoma. Proc. Southeastern Assoc. Game and Fish Comm. 29:415–423.

Mech, L. D. 1970. The wolf: the ecology and behavior of an endangered species. Natural History Press, Garden City, New York.

Schaller, G. B. 1972. The Serengeti lion: a study of predator-prey relations. Univ. Chicago Press, Chicago, Illinois.

Servheen, C. W. 1975. Ecology of the wintering Bald Eagles on the Skagit River, Washington. M.S. thesis, Univ. Washington, Seattle, Washington.

Shea, D. S. 1973. A management oriented study of Bald Eagle concentrations in Glacier National Park. M.S. thesis, Univ. Montana, Missoula, Montana.

Southern, W. E. 1963. Winter populations, behavior and seasonal dispersal of Bald Eagles in northwestern Illinois. Wilson Bull. 75:42–55.

Sprunt, A., IV and R. L. Cunningham. 1962. Continental Bald Eagle project. Progress Rept. No. 2.

——— AND F. J. LIGAS. 1966. Audubon Bald Eagle studies 1960–1966. Proc. Natl. Audubon Soc. Conv. 62:25–30.

STALMASTER, M. V. AND J. R. NEWMAN. 1978. Behavioral responses of wintering Bald Eagles to human activity. J. Wildl. Manage. 42:506–513.

——— AND ———. 1979. Perch-site preferences of wintering Bald Eagles in northwest Washington. J. Wildl. Manage. 43:221–224.

STEENHOF, K. 1976. The ecology of wintering Bald Eagles in southeastern South Dakota. M.S. thesis, Univ. Missouri, Columbia, Missouri.

VERBEEK, N. A. M. 1977. Comparative feeding behavior of immature and adult Herring Gulls. Wilson Bull. 39:415–421.

MISSOURI COOPERATIVE WILDLIFE RESEARCH UNIT, SCHOOL OF FORESTRY, FISHERIES AND WILDLIFE, 112 STEPHENS HALL, UNIV. MISSOURI, COLUMBIA, MISSOURI 65211. ACCEPTED 5 JUNE 1980.

PRESIDENT'S MESSAGE

As part of its efforts to encourage research by students and amateurs The Wilson Ornithological Society sponsors a series of awards. Of these, the two oldest, named in honor of Louis Agassez Fuertes and Margaret Morse Nice, are not supported by endowment. Therefore, their distribution is not guaranteed. The Council and I prefer that support for their endowment be gathered from the membership rather than a single donor. The many small donations would provide a special kind of honor, both for the awards and the recipients, and the awards truly would come from the Society.

Most of you will shortly be returning your 1982 Dues Notice to the Ornithological Societies of North America. I have instructed Treasurer Robert D. Burns that any donations to the Wilson Endowment Fund for 1982 be credited to the Fuertes and Nice Awards. Treasurer Burns would also be happy to accept contributions mailed directly to him. The required amount is about $6,000. The Society has just over 2,250 active members. Hence, a contribution from each of us of only $3.00 would be sufficient.

Two years ago many of the "older" Life Members responded to a plea from then President George Hall with major contributions that helped the Society through a difficult period. I trust the general membership will now respond as generously to this solicitation for a much happier cause.

Abbot S. Gaunt, *President*

Wilson Bull., 93(2), 1981, pp. 265–267

GENERAL NOTES

Interspecific song mimesis by a Lincoln Sparrow.—Some oscines learn the songs of alien species in the laboratory, but in the wild generally learn only conspecific songs (Kroodsma, *in* Ontogeny of Behavior, Burghardt and Bekoff, eds., Garland Publ. Co., New York, New York, 1978). Of those groups which do mimic in nature, finches (carduelids and emberizids) vary in their propensity to imitate heterospecific songs. In Germany, European Greenfinches (*Chloris chloris*) imitate a wide variety of sympatric species and use these imitations in their advertising songs (Guttinger, J. Ornith. 115:321–337, 1974; Baptista, unpubl.). Indigo (*Passerina cyanea*) and Lazuli (*P. amoena*) buntings regularly imitate each other in a zone of sympatry in Nebraska (Emlen et al., Wilson Bull. 87:145–179, 1975). Other species mimic rarely (Baptista, Z. Tierpsychol. 30:266–270, 1972; Kroodsma, Wilson Bull. 84:173–178, 1972; Williams and McRoberts, Condor 79:113–118, 1977).

Several learning strategies appear to exist in *Melospiza*. Swamp Sparrows (*M. georgiana*) exposed to conspecific songs and those of sympatric Song Sparrows (*M. melodia*) learned conspecific songs but failed to mimic interspecifically. Song Sparrows similarly exposed learned their own plus heterospecific songs (Marler and Peters, Science 198:519–521, 1977). Indeed, Song Sparrows are now known to mimic other species both in the laboratory and in the field (Eberhardt and Baptista, Bird-Banding 48:193–205, 1977; Kroodsma, Anim. Behav. 25:390–399, 1977). Lincoln Sparrows (*M. lincolnii*) to our knowledge, have not, hitherto, been known to copy songs of heterospecifics. We document herein a case of interspecific song mimesis in a Lincoln Sparrow and speculate on the conditions leading to this behavior.

In 1978, we began studies on song dialects and their possible function(s) in montane White-crowned Sparrows (*Zonotrichia leucophrys oriantha*) at Tioga Pass Meadow, Mono Co., California, 119°E 38°N, elev. ca. 3000 m. About 25 pairs of White-crowned Sparrows and 2 pairs of Lincoln Sparrows breed on this meadow. On 25 June 1979, we recorded a territorial Lincoln Sparrow whose songs possessed components virtually identical with syllables from a White-crowned Sparrow. Songs of White-crowned Sparrows at Tioga Pass have been studied in great detail (Orejuela and Morton, Condor 77:145–153, 1975; Baptista and King, Condor 82:267–284, 1980). Typically, each song begins with a whistle (Fig. 1A, syllable type a), followed by a buzz (b), a complex syllable (c), a trill (d and e), ending with another buzz (f). The complex syllable (c) shows regional variation. This particular form of syllable (c) illustrated is found at Gardisky Lake, about 4 km north of the meadow. However, several White-crowned Sparrows used this syllable at the meadow and on mountain slopes to the east.

A detailed study of song variation and ontogeny in Lincoln Sparrows is still lacking. Borror (Ohio J. Sci. 61:161–174, 1961) analyzed some Lincoln Sparrow songs from Ontario and Wyoming. He noted that each bird sang 3 or more themes (unique combinations of syllables), and that birds at a locality shared similar or identical phrases. We identified 5 themes in 23 recorded songs from our Lincoln Sparrow (Fig. 1B–F). Each theme consisted of 5–7 syllable types, each of which occurred singly or in groups of 2–8. Three themes contained 4 (Fig. 1B), 2 (Fig. 1C) or 1 (Fig. 1D) syllables in common with White-crowned Sparrow song.

Syllable e (theme B) is similar to a modified White-crowned Sparrow syllable arranged in a trill. Another White-crowned Sparrow (not illustrated) recorded on the study meadow used syllables similar to this type e. The buzz in theme B (syllable b) is more rapidly modulated than any local White-crowned Sparrow buzz. However, similar buzzes are known from songs of other populations of White-crowned Sparrows (Baptista, Univ. Calif. Publ. Zool. 105:1–52, 1975). The 2 terminal syllables in theme B are similar to those in other typical Lincoln Sparrow themes (see theme E).

FIG. 1. A. Song of a White-crowned Sparrow recorded at Gardisky Lake, 4 km north of Tioga Pass Meadow. B–F. Themes sung by a Lincoln Sparrow recorded at the Meadow, 25 June 1979. Note that the Lincoln Sparrow's themes include 0 (themes E and F), 1 (e in theme D), 2 (b and c in theme C), or 4 (b, c, d, e in theme B) syllables borrowed from a White-crowned Sparrow.

It is possible that syllables from songs of different species may be alike accidentally. However, the fact that as many as 4 syllable types in theme B match those of the model (A) in both structure and sequence is strong evidence that song mimesis has occurred.

This Lincoln Sparrow appeared to show considerable improvisation in developing its song repertoire. The introductory whistle typical of all White-crowned Sparrow songs has been replaced by a series of syllables in all its mimicked songs. White-crowned Sparrow syllables were incorporated in 3 themes (B, C and D). The same Lincoln Sparrow syllables were also used in several themes. Thus, as in the congeneric Song Sparrow (Eberhardt and Baptista 1977), Lincoln Sparrows may use the same syllables in different themes.

Several explanations have been postulated for interspecific song mimesis in nature. Large song repertoires may advertise individual fitness. For example, in an habitual mimic, the Northern Mockingbird (*Mimus polyglottos*), repertoire size was correlated with territorial quality (Howard, Evolution 28:428–438, 1974). Since Howard did not age the birds, possibly those with higher quality territories were dominant, reflecting their age and experience. Older birds presumably would have had more time to copy greater numbers of alien species (Dobkin, Z. Tierpsychol. 50:348–363, 1979). Birds hatched late in the year may be exposed to fewer conspecific songs in their acoustic environment and thus mimic interspecifically (Baptista 1972, Kroodsma 1972). Since Lincoln Sparrows are rare on Tioga Meadow, a juvenile developing its vocal repertoire would encounter few conspecifics to imitate and may thus be stimulated to imitate interspecifically. Occasional interspecific mimicry may simply reflect individual variation in dispositions to improvise (Baptista 1972). Interspecific competition may result in convergence of distance producing signals, e.g., territorial song,

through learning interspecifically (Cody, Condor 71:222–239, 1969; Emlen et al. 1975; Brown, Can. J. Zool. 55:1523–1529, 1977).

In territorial species, song learning and matching of themes often follows intense intermale interaction (Bitterbaum and Baptista, Auk 96:462–474, 1979). Nice (Trans. Linn. Soc. 6:1–238, 1943) hand-raised 2 Song Sparrows which vied for dominance, each soon producing 6 identical themes. The closely related Lincoln Sparrow is also highly territorial and responds strongly to playback of conspecific song. We have several observations of the Lincoln Sparrow interacting aggressively with sympatric White-crowned Sparrows and vice-versa. Perhaps the Lincoln Sparrow learned the White-crowned Sparrow's song during such interspecific interaction.

Fieldwork was supported in part by National Science Foundation Grant DEB 77-12980 to Baptista and Morton.—Luis F. Baptista, Martin L. Morton and Maria E. Pereyra, *Dept. Biology, Occidental College, 1600 Campus Road, Los Angeles, California 90041.* (Present address LFB: *Dept. Birds and Mammals, California Academy of Sciences, San Francisco, California 94118.*) *Accepted 20 May 1980.*

Wilson Bull., 93(2), 1981, pp. 267–271

Notes on Purple Gallinules in Colombian ricefields.—Little has been reported on Purple Gallinules (*Porphyrula martinica*) in ricefields, despite the species' affinity for this habitat as a nesting site (Ensminger, La. Conserv. 11:19, 1959; Meanley, Auk 80:545–547, 1963). Descriptions of nests and food habits are few and limited to populations in naturally occurring marshes (e.g., Bent, U.S. Natl. Mus. Bull. 135, 1926; Gross and Van Tyne, Auk 46:431–446, 1929; Imhof, Alabama Birds, Univ. Alabama Press, University, Alabama, 1962). In certain Neotropical areas, Purple Gallinules are considered pests due to loss of harvestable rice incurred by bending rice (*Oryza sativa*) plants into nests and feeding platforms (Feakin, ed., Pest control in rice, PANS Manual No. 3, Tropical Pesticide Research and Information Unit, London, England, 1970). Gallinules are seasonally abundant in much of the extensive rice-producing region east of the Andes in northern South America, prompting experimentation with various control procedures. Endrin has been used as a control agent for gallinules in Surinam (Haverschmidt, Birds of Surinam, Livingston Publ. Co., Wynnewood, Pennsylvania, 1968) and is presently being used in Colombia, but few data are available on the effects of this practice. In this paper, I describe nest abandonment by Purple Gallinules in response to endrin applications, and report on nest construction and placement, observations of an unusual escape behavior, and food habits of the species in Colombian ricefields.

Study area and methods.—The Hacienda La Corocora (3°57′N, 73°24′W; elev. 310 m) is located in a large rice-growing zone in the tropical savanna of the Llanos Orientales in Meta, Colombia. Annual rainfall averages 2600 mm, with the rainy season occurring from April–October. Descriptions of climate and vegetation of the region were given by Bates (Geogr. Rev. 38:555–574, 1948) and Blydenstein (Ecology 48:1–15, 1967). Rice is grown year-round in 10–90 ha plots bordered by marshes and shrubby pastures. Ricefields in various stages of growth occupy a contiguous area of 600 ha with a mean water level of 13.5 cm in cultivated plots. Purple Gallinules migrate to the area in late March and nest from May at least through August. Gallinules are occasionally found in green ricefields, but usually do not enter fields until the "yellowing" or maturing stage, when rice grains are forming (about 10 weeks after germination). As water is drained from each plot prior to harvesting, gallinules move into

nearby ricefields that are beginning to mature. Most gallinules leave the area at the end of the wet season, although small numbers remain all year in local marshes. Little is known regarding dispersal of the migrant population.

I estimated minimum density of gallinules in ricefields by averaging flush counts from parallel 300 × 40-m transects spaced 250 m apart. I sampled 3–5 transects per plot (depending on plot size) on different days to reduce bias associated with birds flushing from one transect to another and being counted twice. Density figures were obtained prior to and following aerial applications of 19.5% endrin (1 gal/ha or 3.79 l/ha) by the Hacienda in 1977 and 1978.

Nests were located by systematically searching ricefields and nearby marshes on repeated occasions during May–July 1977 and 1978. For each nest I recorded height of nest rim above water, greatest diameter of nest, outside depth, bowl depth, estimated percent of nest surface covered when viewed from directly above, size and placement of runway (Gross and Van Tyne 1929) and number and sizes of eggs. I investigated correlates of nest placement in ricefields by recording water depth, height of rice above water and distance to nearest ricefield border at nest-sites and comparing these values with similar data obtained at an equal number of ricefield locations determined from a table of random numbers. I recorded data only from nests known to be active, i.e., containing eggs, since unfinished nests are frequently found near active nests (Bent 1926).

I collected 48 adult-plumaged gallinules in ricefields during May–June 1977 and 1978. Food items removed from the esophagus, proventriculus and gizzard were preserved in 8% formaldehyde (Martin, Procedures in Wildlife Food Studies, USFWS Wildlife Leaflet 325, 1949) and subsequently identified. Aggregate volume of each item was determined by water displacement. Six birds with empty digestive tracts or extensively digested stomach contents were excluded. The remaining sample contained 14 males, 14 females and 14 birds of unknown sex whose digestive tracts had been removed by farm workers before the gonads could be examined.

Gallinule densities and response to endrin applications.—In 1977, migrant gallinules first appeared in marshes on the study area during the last week of March. Numbers increased through April and scattered individuals were observed in the earliest maturing ricefields (an area of 50 ha) during the second week of May. Gallinules became abundant in these plots during the third week of May with a minimum density of 21/ha. This density indicated a large influx of migrants, since the number of birds in the marshes did not appear to decrease. Egg-laying began on 17–18 May. On 2 June, endrin was applied to plots with nesting gallinules. By 3 June, all nests (N = 11) had been abandoned and minimum density of birds had decreased to 2/ha. Many gallinules had apparently moved and begun to nest in untreated plots (area 22 ha) which were beginning to mature. Minimum density in the second plots was 27/ha on 15 June. Endrin was then applied to all untreated plots on 1 July, after which the new nests (N = 18) were abandoned and virtually all gallinules left the Hacienda's ricefields. No dead birds were found following either application. Where the gallinules went is unknown.

In 1978, gallinules appeared in the earliest maturing ricefields during the first week of May, but the large influx of migrants did not occur until the first week of June. Minimum density was 20/ha by 7 June. Endrin was applied to all plots during 9–20 June, after which most gallinules left the area without initiating nests. I found 5 dead gallinules after the 1978 pesticide applications. The birds presumably died from pesticide poisoning, but facilities for analysis were not available. Although gallinules remained in ricefields at low densities (7/ha) until I left the study area in mid-August, I found only 1 nest in 1978, which was abandoned by 1 July.

Nests and eggs.—All ricefield nests (N = 30) were constructed entirely of leaves and panicles of growing rice plants wound into a roughly circular cup supported by rice stems.

Platforms were numerous in the vicinity of nests, but nests were not located on these structures. Nests had a mean diameter of 21.8 ± 0.4 (SE) cm (range 16–28 cm), outside depth of 10.0 ± 0.5 cm (6–16 cm), bowl depth of 5.2 ± 0.4 cm (2–9 cm), and were placed 29.8 ± 1.0 cm (21–42 cm) above the water. Most nests were partially covered by leaves and panicles bent over into a high arch 25 cm or more above the nest rim. Surface areas of 3 nests were covered 50% or more, 10 nests were 25–50% covered, 7 were 10–25% covered, 6 were 1–10% covered and 4 were not covered to any extent. Most nests had an entrance indicated by a low section of the rim adjacent to a runway of bent leaves which often led to feeding platforms. Runways were approximately 15 cm wide, 20 cm–1+ m long and either led directly to the entrance or were built tangentially to it, apparently allowing the birds to enter the nest from 2 directions. Several runways were poorly-defined, and 3 nests lacked evidence of runways or entrances.

Nest-site means for water depth (14.7 ± 0.8 cm, range 6–26 cm), rice height (65 ± 1.3 cm, 55–85 cm) and distance to nearest border (108 ± 16.7 m, 29–200 m) did not differ from those for 30 random points ($t = <1.7$), indicating that gallinules nested randomly with respect to these factors. Data regarding nest spacing are incomplete, since more nests would probably have been initiated if endrin had not been applied. Observed inter-nest distance was usually 40 m or more, although 2 nests were located only 11 m apart.

Clutches contained up to 7 eggs, but many nests were obviously abandoned before clutches were complete (13 nests contained 1–2 eggs). Fifty-three eggs averaged 41.0 ± 0.3 × 29.3 ± 0.2 mm. Eggs within clutches varied by as much as 5.5 mm in length and 2.5 mm in width. Weights of 2 eggs of unknown age were 15.2 g and 14.8 g.

Seven additional nests were found in dense growths of "platanillo" (*Thalia geniculata*) in narrow strips of marsh habitat (<0.5 ha) along streams and drainage canals. Nests were constructed of *T. geniculata* leaves and differed from ricefield nests by being placed at greater heights above the water ($\bar{x} = 56.7 \pm 5.0$ cm, $t = 2.80$, $P < 0.01$), and having greater outside depths ($\bar{x} = 15.6 \pm 1.9$ cm, $t = 2.77$, $P < 0.01$). No more than 1 nest was found in each area of marsh.

Escape behavior.—When approached, gallinules usually flushed, although they frequently remained on the ground and moved away through the vegetation. On several occasions, I closely pursued running gallinules whose locations were apparent from movements of the rice plants. After running several meters, the birds that did not flush lowered their bodies 2–3 cm under the water, flattened out and remained completely submerged with eyes closed. I captured by hand male and female birds in this submerged posture. Local farm workers often use this technique to catch gallinules for food. To my knowledge, this unusual escape behavior has not been reported for the species.

Food habits.—Rice grains constituted 68% of the food by volume, occurring in all but 1 of the stomachs examined (Table 1). The remainder comprised ricefield weed seeds (5%) and animal matter (27%), the most frequent being borer moth (Noctuidae) pupae and larvae, dragonfly (Odonata) adults and nymphs, and various beetles (Coleoptera). An unusual item was a 2.6-cm section of the unfeathered crus and knee of an adult-sized Purple Gallinule, found in the gizzard of a female collected 26 June 1977. This was presumably taken from a dead bird, implying that gallinules occasionally will feed on carrion. On 2 occasions, I found partially-eaten sections of 10-cm fish (Cichlidae) on feeding platforms. Grit, obtained from adjacent gravel access roads, was present in all stomachs examined.

Purple Gallinules are known to feed largely on seeds and fruit of aquatic plants supplemented by small invertebrates (Gross and Van Tyne 1929; Imhof 1962; Krekorian, Condor 80:382–390, 1978), although feeding on flower blossoms (Crosby, Florida Nat. 42:171, 1969), tree fruit (Meanley 1963) and opportunistic predation on eggs and young of other birds (Bailey, Auk 44:560, 1927; McIlhenny, Auk 53:327–328, 1936; Beadel, Auk 63:87–88, 1946) have also

Table 1

Esophageal and Stomach Contents of 42 Purple Gallinules Collected in Colombian Ricefields May–June 1977 and 1978

Food item	Percentage	
	Volume	Occurrence
Plant (seeds)		
Rice, *Oryza sativa*	68	98
Cyperaceae spp.	2	19
Paspalum notatum	1	5
Thalia geniculata	trace	5
Panicum sp.	trace	2
Echinochloa colonum	trace	5
Scleria pterota	trace	2
Polygonum sp.	trace	7
Gramineae sp.	trace	2
Scirpus sp.	trace	7
Croton tinctoria	trace	2
Paspalum virgatum	trace	7
Total plant	73[a]	98
Animal		
Noctuidae pupae and larvae	14	12
Odonata adults and nymphs	6	12
Coleoptera (undetermined)	1	10
Curculionidae	1	7
Tenebrionidae	trace	5
Hemiptera (undetermined)	trace	2
Pentatomidae	trace	2
Corydalidae larvae	trace	2
Cyclorrhapha pupae	trace	2
Hymenoptera	trace	2
Other insect (undetermined fragments)	4	26
Arachnida	trace	5
Gastropoda	trace	2
Crus-knee segment (gallinule)	1	2
Total animal	27[a]	43

[a] Totals include trace (>0.5%) items.

been reported. This study demonstrates that gallinules nesting in ricefields feed mostly on rice, but take a variety of other items when available.

Sexes did not differ in amounts of rice or plant material eaten, but females consumed greater volumes of animal matter ($\bar{x}$ = 1.9 ml for females vs <0.1 ml for males, $t = 2.42$, $P < 0.05$) and total food ($\bar{x}$ = 6.2 ml vs 3.6 ml, $t = 2.07$, $P < 0.05$). Mean weights of males (213.4 ± 5.1 g) and females (223.6 ± 15.6 g) were not significantly different (t-test, NS). Sexual differences in food habits may correspond to selection by females for more animal

matter during the nesting season. For birds in general, egg production requires more protein than does sperm production (King, pp.79–107 *in* Breeding Biology of Birds, Farner, ed., Natl. Acad. Sci., Washington, D.C., 1973). Krekorian (1978) assumed that the heavier bird in each pair was male; the lack of significant sexual dimorphism in the weight of breeding Purple Gallinules in this study suggests that this may not be a reliable criterion for sexing the birds.

In eastern Colombia the amount of land converted to rice culture is steadily increasing. Ricefields present an advantageous nesting habitat for Purple Gallinules by affording an abundant food supply and stable water levels. Some of the insects consumed by gallinules are serious pests in rice (notably the noctuid caterpillars), indicating that food habits of this species are to some extent beneficial. I was informed by local farmers that endrin is used against gallinules in varying quantities and apparently with no established guidelines. Little is known regarding the effect of pesticides of gallinule population dynamics. In view of the potential for crop and environmental contamination, studies integrating damage analysis with feeding habits are needed to assess accurately the impact of Purple Gallinules in tropical ricefields.

This study was sponsored by the Instituto Colombiano Agropecuario. I am grateful for the assistance of Danilo Valencia, Ernesto Barriga, Dario Leal and La Corocora Ltda.; I especially thank Patricia Chacón for identifying insects. E. E. Good, Thomas Lemke, Jeffrey Jorgenson and Clait Braun offered valuable advice on drafts of this manuscript.—Wallace D. McKay (deceased), *Smithsonian-Peace Corps Environmental Program, U.S. Embassy, Bogotá, Colombia.* (Corresponding address: Douglas McKay, *17 Hamilton Ave., Wheeling, West Virginia 26003*). *Accepted 20 Mar. 1980.*

Wilson Bull., 93(2), 1981, pp. 271–274

Agonistic behavior of the White-breasted Nuthatch.—My studies of agonistic behavior of White-breasted Nuthatches (*Sitta carolinensis*) were begun in Bethesda, Maryland, in 1953, but generally undertaken in Lyme, New Hampshire, between 1961 and 1973. Previous detailed reports of agonistic behavior of the White-breasted Nuthatch are lacking, although Tyler (Wilson Bull. 28:18–25, 1916), Butts (Bird-Banding 2:1–26, 59–76, 1931), Bent (U.S. Natl. Mus. Bull. 195, 1948) and Brackbill (Maryland Birdlife 25:87–91, 1969) have been helpful.

Agonistic displays.—Included are a spectrum of displays which, as noted for the European Nuthatch (*S. europaea*) (Löhrl, Z. Tierpsychol. 15:191–252, 1958), may merge confusingly. Displays most discernible are:

(1) Tail-fanning. Here the tail is raised and fanned, displaying the black and white markings. It is given frequently by the female when her mate comes close to the nest where she is dominant, as well as in conflicts with rival pairs.

(2) Wing-flicking. This action, combined with raising the tail, was used chiefly against predators.

(3) Threat display. Usually the bill is raised, wings are down and tail is cocked up as shown in Fig. 1 and by Löhrl (1958) for the European Nuthatch. The pose is assumed by a subordinate when threatened by a dominant bird of the same or a different species.

(4) Aggressive threat display. It resembles (3), except for a raising of the back feathers and a pointing downward of head and bill (Fig. 2). It is given in severe conflicts.

(5) Raising back feathers with wings and tail in normal position. This display (Fig. 3) is

FIG. 1. Threat display of a White-breasted Nuthatch.

usually seen just prior to one nuthatch attacking another, as when a male is about to fly at his mate prior to a pursuit flight (Kilham, Auk, 89:115–129, 1972).

(6) Bill pointed forward. A female runs with bill pointed straight forward without any display, either at a male intruder by the nest or at a juvenile she is trying to drive away.

Displacement pecking. Males excited in border conflicts (or, as one seen when disturbed by a Barred Owl [*Strix varia*]), will occasionally peck at places unconnected with food, the head and bill held straight up and down. Brackbill (1969) noted this activity among nuthatches coming to a tray where other birds were feeding. I interpreted it as a displacement activity in which a drive to attack is both activated and thwarted, the pecking being a way of relieving surplus excitation (Bastock et al. Behaviour 6:66–84, 1953).

Vocalizations.—Several kinds are involved as follows:

Tchup expresses mild excitement. *Kun*, *ka-un* and *kaan* all express excitement (Kilham 1972), the degree depending on whether they are loud or soft, or given singly or in a rapid series. As with *tchup*, the excitement may be from any cause.

FIG. 2. Aggressive threat display.

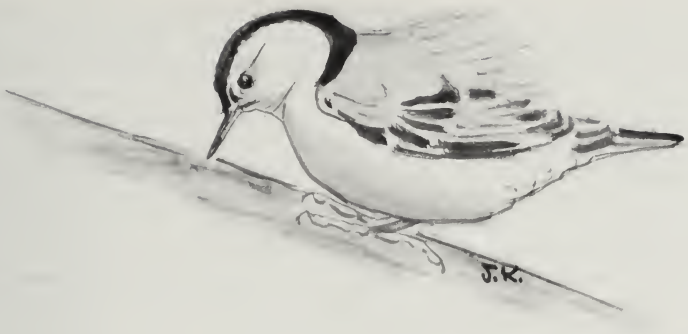


FIG. 3. About-to-attack display.

Grr, grr-n. Various notes take on a harsh quality with an *rr* sound when a nuthatch is aroused by a rival or predator in or out of the nesting season. A nuthatch may start giving them without apparent cause. However, White-breasted Nuthatches can be aroused by a distant rival that is not always perceptible to a human observer.

Brr-a. I have heard this note given by nuthatches coming to a feeding tray, apparently as a warning (territorial) to Black-capped Chickadees (*Parus atricapillus*) or conspecifics.

Medley-of-notes-in-conflict. Mixtures of the vocalizations of 3 or 4 nuthatches in conflict may become staccato or even musical, and include a *qua* or quavering *qua-rr* heard only then.

Agonistic song.—This is a rapid series of *hn-hn* notes generally confined to the breeding season (January–June), regarded by Tyler (1916) as the rarely heard second main song of this species. I heard this song only in agonistic situations. On 17 January, a male made a continuous series of these notes, almost like a buzzer, when close to a Barred Owl. Another male gave these notes several times when I was 6 m from a nest, as if he regarded me as an intruder.

The agonistic song appears at times to be a combination of agonistic and courtship behavior, corresponding to a similar song of the Red-breasted Nuthatch (*S. canadensis*) (Kilham 1973). In *S. carolinensis*, this song usually requires a setting similar to that in which courtship song occurs (i.e., usually early in the day with the female resting close by), plus the presence of a rival at a distance.

Territory and territorial encounters.—White-breasted Nuthatches, even deep in their own territory, appear aware of neighboring pairs. At 06:00 on 10 April, the members of a pair were exchanging low *hit-tucks* when the male switched to *hn-hn* notes. Both sexes then made loud *kun* and *ka-uns* as they flew to the nearest border. I heard a second pair there, but the 2 pairs quickly separated. Other encounters, arranged below by order of severity, were of greater duration.

Grade I. Two severe encounters were in March. At 06:10 on 31 March, the members of 2 pairs were all in aggressive threat displays in a hornbeam (*Carpinus*). The 2 males flew at each other, fluttering beak to beak in midair.

Grade II. At 09:00 on 7 December, a different pair of nuthatches each moved 2–3 m above the gound in saplings on either side of a dirt road. All 4 birds gave aggressive threat displays and uttered a mixture of notes, including buzzer-like *grrs*. Each male remained on his side, only the females crossed over. Whenever a female returned to her mate both birds started displacement pecking. The conflict, occuring before the onset of active courtship, primarily involved the females.

Relation of territorial conflicts to pair bond.—In some species (e.g., Hairy Woodpecker [*Picoides villosus*]) (Kilham, Wilson Bull. 81:169–183, 1969), the pitch of emotion aroused against a rival can be diverted to courtship during lulls in territorial conflict. This antecedent situation was seldom evident for *S. carolinenesis*. On a number of occasions there was an increase in intimate, antiphonal notes between members of pairs following conflicts. I also once saw courtship feeding after a conflict. Generally, however, there were no indications that agonistic behavior stimulated courtship. Severe conflict appeared to have the opposite effect. In some instances, a male attacked his mate during lulls in fighting with a rival, behavior also noted by Löhrl (1959) in *S. europaea*. This would seem to be a case of redirected attack in the sense used by Bastock et al. (1953).

Size and nature of territories.—By following limits of wanderings as well as noting location of conflicts, I estimated that 1 pair of nuthatches had a territory of 15 ha, approximating that given by Brackbill (1969) for a banded pair in Maryland.

Effects of a feeding station.—A feeder with suet and sunflower seeds in the territory of 1 pair in the winters of 1968 and 1969 attracted a second pair whose territorial boundary was only 12 m away. Efforts of the second pair to enter the territory of the first pair led to daily conflicts. The second pair usually gave threat displays when they were by their territorial border and trying to reach the feeder. The male not only drove away the intruders, but often his own mate as well. The feeder disrupted the daily movements of the chickadees and nuthatches to such an extent that studies of natural behavior became impossible. Interestingly, Bock (Ecology 50:903–905, 1969), in discussing White-breasted as well as Pygmy (*S. pygmaea*) nuthatches, stated that: "The artifact of having an abundant food source of precise and predictable localities caused a breakdown in flock organization and a rapid sort of 'competitive exclusion' at the feeders." Present studies were made in woods away from feeders.

Reactions to predators.—The most intense reaction witnessed was at 16:00 on 17 January, when a male nuthatch stayed within 5–7 m of a Barred Owl, alternating bouts of displacement pecking with rapid *hn-hns*. The nuthatch's tail was raised slightly and he occasionally flicked his wings. A pair of Hairy Woodpeckers, present part of the time, also engaged in displacement pecking. Perhaps the intensity of the nuthatch's reaction may have been due to the lateness of the afternoon and the proximity of the owl to the nuthatch's (and the woodpecker's) roosting place.

A male nuthatch travelling with chickadees and a Brown Creeper (*Certhia familiaris*) on 2 March encountered a Barred Owl dozing in the open. The male uttered *kun* and harsh *kaan* notes, but did not come close. After 1–2 min the flock departed. Possibly sleepy owls at mid-day evoke different reactions than alert ones at dusk.

Acknowledgments.—I thank my wife, Jane Kilham, for drawing the illustrations.—Lawrence Kilham, *Dept. Microbiology, Dartmouth Medical School, Hanover, New Hampshire 03755.* *Accepted 20 Mar. 1980.*

Wilson Bull., 93(2), 1981, pp. 274–275

Evasive behavior of American Coots to kleptoparasitism by waterfowl.—On 17 April 1976, at Dewey's Pasture Wildlife Management Area in northwestern Iowa, I saw American Wigeons (*Anas americana*) and Gadwalls (*Anas strepera*) kleptoparasitizing American Coots (*Fulica americana*). One or 2 wigeon or Gadwalls, but not both species at once, closely attended and followed a coot. At times all the coots present (15–25) were attended by kleptoparasites. Both duck species dabbled at vegetation brought to the surface by coots

and stole vegetation directly from the bills of the coots. This note discusses the evasive behavior exhibited by coots when being kleptoparasitized.

Food piracy by Gadwalls has not been previously noted. Wigeon have been reported stealing food from coots (Munro, Can. J. Res. 27:289–307, 1949; Hellyer, Pac. Search 11:26–27, 1977; Knapton and Knudsen, Can. Field-Nat. 92:403–404, 1978), but aggressive or evasive behavior by coots when being kleptoparasitized has not been reported.

The coots I watched (at distances between 35–90 m with a spotting scope) were not aggressive toward their kleptoparasites, but some of them did make evasive maneuvers. When followed by wigeon or Gadwalls, coots dived, brought plant material to the surface, dropped it, swam several meters away and quickly dived again. By dropping the vegetation from the first dive, coots seemingly gained time to dive again and feed unmolested. The wigeon or Gadwalls fed on the plants from the first dive until it was consumed or sank and then pursued the coot again. If sufficient food for the waterfowl was brought to the surface and they were distracted by it, the coot successfully evaded them. When a coot did evade its kleptoparasites, the waterfowl sought out another coot host. During the 2 h that I watched the interactions, food-dropping was rarely successful in allowing coots to completely evade the kleptoparasites. Coots that did not drop food for the waterfowl and attempted to evade them solely by swimming away were not successful.

This evasive behavior is costly in time and energy. Coots attended by kleptoparasites dived more often (median = 4/min, N = 19, range 1–6) than did coots foraging alone (median = 3/min, N = 19, range 1–4, $P < 0.002$, Mann-Whitney U-test) on the same wetland. If, by leaving the food from the first dive, coots were successful in evading further kleptoparasitism, the strategy is advantageous. Even if the waterfowl were not distracted, if more than half of the food collected during each dive was stolen, it would be advantageous for the coots to leave the food from 1 dive for their kleptoparasites and to feed unmolested on the next dive.

Because many studies have noted the high intensity of interspecific aggressiveness in coots (e.g., Gullion, Condor 55:169–186, 1953; Ryder, Auk 76:424–438, 1959; but see Ryan and Dinsmore, Auk 96:704–713, 1979), the lack of aggression toward kleptoparasites is surprising. Several factors suggest that outright aggression may be less effective than the food-dropping strategy. Aggression may be ineffective because, even if driven off before a foraging dive, nothing prevents the kleptoparasite from returning and stealing food when the coot resurfaces. Knapton and Knudsen (1978) noted the importance of food piracy to wigeon when the only vegetation available was in deep water, as was true in the spring when I made my observations. Opportunistic kleptoparasitism may make the waterfowl tenacious in their piracy attempts and might result in the coot food resources being economically non-defendable. It may also be energetically too costly for coots to defend their food from several attending pirates, the kleptoparasites effectively swamping the aggression.

This is Journal Paper J-9495 of the Iowa Agriculture and Home Economics Experiment Station, Ames, Iowa, Project No. 2170. Observations were made while I was supported by the Iowa Agriculture and Home Economics Experiment Station and grants from the Frank M. Chapman Memorial Fund, American Museum of Natural History and Sigma Xi. I thank J. J. Dinsmore, M. G. Henry, P. A. Heagy, L. H. Fredrickson, C. Braun and J. C. Barlow for their criticisms of an earlier draft of this note. This is contribution No. 4 of the Avian Research Laboratory, Department of Animal Ecology.—Mark R. Ryan, *Dept. Animal Ecology, Iowa State Univ., Ames, Iowa 50011.* *Accepted 29 Jan. 1980.*

Wilson Bull., 93(2), 1981, pp. 276–277

Additional evidence of egg-moving behavior by female Gadwalls. —Johnson and Kirsch (Wilson Bull. 89:331–332, 1977) noted moving of eggs between nest bowls by a female Gadwall (*Anas strepera*) in North Dakota. This note documents additional evidence of such behavior and suggests that egg moving may be more frequent in this species than previously indicated.

During a study of the Gadwall in southern Manitoba, 188 females were trapped on the nest, using a modification of the automatic nest trap originally designed by Weller (J. Wildl. Manage. 21:456–458, 1957). From 1973 through 1975, 12 instances of egg moving were recorded in which the female moved all or portions of the original clutch from within the trap to another nest bowl outside (Table 1). Two instances involved moving of eggs in 2 successive trapping attempts.

In this study, moving of eggs appeared to be the result of an improper trapping technique at the nest-site. The capture method relied on the correct orientation of the trap entrance to the most frequently used approach path of the hen to the nest bowl. Once inside, the female tripped the door release and was captured. However, the placement of the closed portion of the trap over the path probably resulted in the accidental release of the door while the female was still outside the trap. I suspect that the female then moved the eggs by pulling them through the 5.1 × 5.1 cm (2 × 2 in) mesh of the trap with the underside of its bill. Most of the eggs were removed through the mesh of the trap cylinder. However, 2 cases were recorded in which the female appeared to roll the eggs out of the open door. In both instances, the female was captured after removing part of the clutch.

Eight Gadwall hens were captured from these nests and aged as yearlings (1 year old) or

Table 1

Summary of Egg Moving and Other Nest Data for Female Gadwalls in Southern Manitoba, 1973–1975

Year	Age of female	Clutch-size	Stage of incubation	No. of eggs moved
1973	Yearling[a]	8	19	8
	Yearling[a]	8	20	8
	Adult	7	18	7
	Yearling	10	20	2
	Unknown	8	4	2
	Adult	10	14	10
1974	Adult	7	25[c]	1
	Adult	12	8	6
	Unknown[b]	9	21	9
	Unknown[b]	9	22	9
	Adult	8	24[d]	8
1975	Yearling	9	22	9

[a] Same female.
[b] Same female.
[c] One egg in the original nest bowl was partially hatched.
[d] All eggs were pipped.

adults (2 years old or older) (Blohm, M.S. thesis, Univ. Wisconsin, Madison, Wisconsin, 1977). Eggs were aged to the nearest day to determine the stage of incubation when moved. No relationship appeared to exist between clutch-size, stage of incubation, or age of the female and the occurrence of egg moving in this study. Lorenz and Tinbergen (Z. Tierpsychol. 2:1–29, 1938), Sowls (Prairie Ducks, Stackpole Co., Harrisburg, Pennsylvania and Wildl. Manage. Inst., Washington, D.C., 1955:101), Oring (Auk 81:88–89, 1964) and Prevett and Prevett (Auk 90:202–204, 1973) have observed other species of waterfowl retrieving displaced eggs with the ventral portion of the bill. I suspect that this behavior is not uncommon in the Gadwall, especially in situations in which it is necessary to move all or portions of the clutch short distances because of natural or man-made disturbances.

Fieldwork was supported by the Delta Waterfowl Research Station and the University of Wisconsin. I thank R. A. McCabe for his comments on this note. I am indebted to the owners of East Meadows Ranch, the Peter Curry and Arthur Vincent families and to Lawrence King, manager, for their generosity during my stay at Marshy Point, Manitoba. I owe special thanks to all those who assisted me in the field during this study.—Robert J. Blohm, *Dept. Wildlife Ecology, Univ. Wisconsin, Madison, Wisconsin 53706.* (Present address: *Office of Migratory Bird Management, U.S. Fish and Wildlife Service, Laurel, Maryland 20811.*) *Accepted 27 May 1980.*

Wilson Bull., 93(2), 1981, pp. 277–278

Mallard using moving vehicles for predator avoidance.—Distraction displays are often-cited adaptations for predator avoidance in a variety of vertebrate organisms (see Eibl-Eibesfeldt, Ethology—the Biology of Behavior, Holt, Rinehart and Winston, Inc., New York, New York, 1975). Examples of such behavior commonly relate to use of body appurtenances (i.e., feather-ruffling, break-away tail) and less often to use of extrinsic environmental features. We report here an apparent attempt by a duck to use moving vehicles as a distraction during predator avoidance.

In mid-afternoon on 21 January 1977, we were driving south-west on Interstate Highway 90 about 12 km NE of Vantage, Grant Co., Washington, when a female Mallard (*Anas platyrhynchos*) appeared suddenly over the left front of the car, flying about 2 m above the roadway. We were traveling 80–85 km/h when the duck passed us rocking slightly from side-to-side as if preparing to land on the roadway. Within 2 or 3 sec a Prairie Falcon (*Falco mexicanus*, age and sex unknown) stooped at the duck from a position above and to the left rear. This stoop was aborted and the Mallard continued flying along the highway 1–4 m above the surface, weaving left to right between several cars, very close to the vehicles. The falcon appeared to hit the duck during the second stoop because the duck tumbled to the ground on the right side of the highway. This attack occurred about 2 km from the point where we initially saw the duck.

The downed duck moved to unmowed roadside vegetation dominated by big sagebrush (*Artemisia tridentata*), Russian thistle (*Salsola kali*) and cheatgrass (*Bromus tectorum*) during which time the falcon made several more stoops without contacting the duck. As we approached and stopped near where the duck had gone down, the falcon flew across the highway from the downed duck and perched on a high voltage pole about 80 m away. We left the car and walked perhaps 15 or 20 m when the Mallard flushed from under a big sagebrush and flew NE with no visible injuries or flight impairment. While we looked for the duck, the falcon left its perch in an unknown direction and did not initiate another attack before the duck flew out of our sight.

It is possible that the Mallard was never hit by the falcon as Dekker (Can. Field-Nat. 94:371–382, 1980) has suggested that erratic plunging flight routinely exhibited by waterfowl when pursued by falcons may appear like a "hit" when in fact no contact is made. The lack of apparent injury to the duck seemingly supports Dekker's suggestion. However, the Mallard was definitely harassed during this episode as evidenced by its speed which approached the maxima of 80–96 km/h previously reported by Cottam (Wilson Bull. 54:121–131, 1942) and Cooke (U.S. Dept. Agric. Circ. 428, 1937). The weaving among cars likely reduced the opportunities for stoops by the falcon for an extended distance along the roadway. Thus, the combination of rapid flight and maneuvering among cars at least prolonged the predator avoidance for this duck and aided its survival (albeit we were the final distracting factor). Whether the cars were used by the duck as a surrogate "flock" is a matter for speculation.

U.S. Army Corps of Engineers Contract No. DACW68–76–C–0184 supported travel during which this observation was made. R. K. Stocker and C. Taylor also witnessed this event. A. J. Erskine and G. Barber provided helpful comments on earlier drafts.—BRUCE C. THOMPSON AND JAMES E. TABOR, *Washington Dept. Game, Olympia, Washington 98504.* (Present address BCT: *Dept. Wildlife and Fisheries Sciences, Texas A&M Univ., College Station, Texas 77843.*) *Accepted 24 Apr. 1980.*

Wilson Bull., 93(2), 1981, pp. 278–279

Ochraceous Wren fails to respond to mobbing calls in an heterospecific flock.— On 6 October, 1970, I was following a mixed-species foraging-flock through a tract of Lower Montane Wet Forest at Monteverde, Puntarenas Province, Costa Rica (see Buskirk and Buskirk, Am. Midl. Nat. 95:288–298, 1976; Powell, Auk 96:375–390, 1979 for descriptions of this location). The flock had just passed me when 2 Common Bush-Tanagers (*Chlorophingus ophthalmicus*), trailing behind the flock, discovered a tree viper (*Bothrops lateralis*) and began giving high-intensity, rapid twitters. Within 30 sec 2 Golden-crowned Warblers (*Basileuterus culicivorus*) and 2 Slate-throated Redstarts (*Myioborus miniatus*), all of which had recently passed the snake, returned and joined the mobbing bush-tanagers 0.5–1.0 m from the snake. Within another 30 sec a Black-and-White Warbler (*Mniotilta varia*), a Wilson's Warbler (*Wilsonia pusilla*) and 2 Ochraceous Wrens (*Troglodytes ochraceus*) arrived. The warblers actively joined the mob. But the wrens remained a few meters away and foraged normally, searching the surfaces of major branches. The behavior of a wren in my line of vision gave no indication that it recognized the presence of the snake or the meaning of the mobbing activity. When the wren approached within 1.5 m of the snake, the wren looked up from its foraging and at the snake. The wren froze for an instant and then began uttering high-intensity calls and joined the mobbing. Immediately the second wren joined the group. The wrens had returned with the flock but had not reacted to the predator until one of them saw it. In all, the mobbing lasted only about 3 min before the flock moved away from the snake.

This incident demonstrates different responses among species to the mobbing calls of other species with which they flock. The wren had not shown unusual excitation or orientation toward the viper prior to its own discovery of the snake. The immediate response of the second wren once the first gave mobbing calls demonstrates intraspecific recognition of such a signal. That wrens returned with the flock suggest they do respond positively to visual and/or auditory cues of the other species. However, the behavior of their associates elicited gregariousness, not alarm.

Several investigators of heterospecific flocks have cautioned that the potential advantages and disadvantages derived from flocking may differ among participants (e.g., Moynihan, Smithson. Misc. Coll. 134:1–140, 1962; Morse, Ecol. Monogr. 40:119–168, 1970). The different behaviors of the wrens and their associates substantiate this caution.

The potential advantages of flocking include the greater surveillance capability of the group and the corresponding benefits of early warning and foraging efficiency (Powell, Anim. Behav. 22:501–505, 1974). The advantage of early warning depends on appropriate response to predator-alert signals.

If, however, "alarm" and/or mobbing calls are prey-to-predator communication of recognition/alertness and thereby identify reduced vulnerability (Buskirk, unpubl.), then predators may avoid hunting in areas where an alarm or mobbing has been given (e.g., Trivers, Q. Rev. Biol. 46:35–57, 1971). If so, some advantage to flock participation may exist for gregarious species not cued to the full information content of these signals. Essentially, a protective "halo" would exist around an alerted flock. A large proportion of flock attendants cannot be of this type or predators will find successful hunting in the vicinity of grouped calls. Eliciting mobbing to attract these unaware but gregarious species or individuals may be a successful hunting ploy for some predators. Smith (Ibis 111:241–243, 1969) found forest falcons (*Micrastur*) provoking mobbing as a hunting technique. Flock attendants, like the wrens, that are unresponsive to the "predator-present" context of these calls should be more vulnerable than the others. Their frequency of attendance in flocks should be optimized at relatively low levels if anti-predation advantages are a predominant selective force for heterospecific gregariousness.

J. Iverson, L. Baptista and E. Tramer provided helpful comments on early drafts. This observation was made during studies supported by a pilot study grant (No. 70–17) from the Organization for Tropical Studies, a Frank M. Chapman Grant from the American Museum of Natural History and a NSF grant (GB–17180) to the University of California, Davis.—William H. Buskirk, *Biology Dept. and Joseph Moore Museum, Earlham College, Richmond, Indiana 47374.* *Accepted 13 Apr. 1980.*

Wilson Bull., 93(2), 1981, pp. 279–280

Fish attack on Black Guillemot and Common Eider in Maine.—Data on bird mortality at sea are scarce and, although predation and scavenging by marine organisms are assumed, few cases have been documented. The subject was generally reviewed by Glegg (Ibis 87:422–433, 1945; Ibis 89:433–435, 1947). Additional reports include predation or scavenging by grey seals (*Halichoerus grypus*) (Grant and Bourne, Seabird Rep. 52–53, 1971; Kinnear, Scot. Birds 9:342, 347, 1977), octopuses (*Octopus* sp.) (Hindwood, Emu 64:69–70, 1964), sharks (*Galeocerdo cuvieri, Carcharodon carcharias, Carcharinus leucas, C. longimanus*) (Brooke and Wallett, Ostrich 47:126, 1976; Dodrill and Gilmore, Auk 95:585–586, 1978; Harrison, Oceans 5:25–26, 1979), monkfish (*Squatina squatina*) (Davenport, Br. Birds 72:77–78, 1979) and cod (*Gadus macrocephalus*) (Scheffer, Murrelet 23:17, 1942). Foot and leg damage is fairly common in some seabirds and has been assumed to represent attempted predation, probably by fish. The following account documents 1 source of foot and leg damage on the coast of Maine.

On 11 August 1975, a newly fledged Black Guillemot (*Cepphus grylle*) and 2 eclipse-plumaged Common Eider drakes (*Somateria mollissima*) were observed being attacked by several fish off Eastern Egg Rock, Muscongus Bay, Maine. The sea was extremely calm,

making disturbances at the surface very conspicuous. The guillemot was first observed being tugged repeatedly under water and immediately bobbing back to the surface. After each tug the guillemot flapped its wings against the surface of the water, but seemed unable to take flight. The flapping propelled the guillemot forward only 4–6 m at a time. The surface was continually disturbed by what appeared to be about 3 fish approximately 0.75 m long. The appearance of the dorsal and caudal fins, overall size, manner of surface-feeding, locality and season suggested bluefish (*Pomatomus saltatrix*), but this could not be verified. The attack was occasionally discontinued for periods of several minutes, during some of which fish attacked the 2 eclipse-plumaged Common Eider drakes nearby. The eiders flapped their wings, ran across the water and eluded the fish for short distances only to be attacked again as soon as they settled on the water. The eiders were eventually able to escape harassment, but the guillemot appeared disabled.

The attack on the guillemot was observed for 1 h. When last seen the guillemot was drifting toward Eastern Egg Rock, where presumably the same bird was found beached the next morning. Both legs had numerous lacerations and the webbing was pierced in several places. These injuries had severed the main tendons on both legs, leaving them completely paralyzed, but the bird was otherwise unharmed and apparently healthy.

Eastern Egg Rock has been occupied by seabird researchers each summer from 1974 through 1979. On 2 August 1974, another immature Black Guillemot was found with similar leg injuries and on 20 August 1974 an adult drake Common Eider in eclipse plumage was found similarly disabled. These 2 birds also appeared healthy but their legs were paralyzed due to severed tendons.

I gratefully acknowledge S. W. Kress for reviewing the manuscript and the Fratercula Fund of the National Audubon Society for providing funding and logistical support that made the field work possible.—THOMAS W. FRENCH, *Atlantic Center for the Environment, 951 Highland Street, Ipswich, Massachusetts 01938.* *Accepted 25 Apr. 1980.*

Wilson Bull., 93(2), 1981, p. 280

Crows steal golf balls in Bangladesh.—The omnivorous Large-billed Crow (*Corvus macrorhynchos*) is widespread in Bangladesh and occurs commonly in towns and villages. In Dacca, this crow and the House Crow (*C. splendens*) serve as important means of helping keep the city sanitary by scavenging on animal and vegetable materials. It is commonplace to observe a mixed flock of 25–100 crows scrambling through a fresh pile of trash on the street.

On 2 December 1978, while at the Dacca Golf Course, I struck a golf ball about 50 m from the green. As the ball descended to an altitude of about 30 m, a Large-billed Crow flew from nearby, seized the ball in mid-air and fled. On the same green I chipped a ball to within 1 m of the hole, only to have a second large-bill flee with the ball.

Such occurrences are common in Dacca and golf enthusiasts must either give up the sport or tolerate crows. Young boys are hired and stationed along fairways to frighten crows during golf matches.

I was unable to determine if the observed crow behavior occurred because the balls were mistaken for food or if the behavior was a manifestation of the tendency of this species, in the words of Ali and Ripley (Handbook of the Birds of India and Pakistan, Vol. 5, Oxford Univ. Press, Bombay, India, 1972:257), to indulge in "puckish pranks, apparently with no object other than fun, such as surreptitiously tweaking its fellows' wing-tips or toes, or a sleeping dog's tail . . . ."—RICHARD M. POCHÉ, *Route 2, Box 164, St. Martinville, Louisiana 70582.* *Accepted 10 Feb. 1980.*

Wilson Bull., 93(2), 1981, pp. 281–282

Notes on the status of the Common African Waxbill in Amazonia.—The Common African Waxbill (*Estrilda astrild*), a species widespread south of the Sahara in its native Africa (Hall and Moreau, An Atlas of Speciation in African Passerine Birds, Br. Mus. Nat. Hist. Publ. No. 780, 1970), is the only exotic bird other than the Rock Dove (*Columba livia*) and the House Sparrow (*Passer domesticus*) (Smith, Condor 75:242–243, 1973; Condor 82:109–110, 1980), to have adapted successfully to Amazonia. *E. astrild* has also been introduced in the Cape Verde Islands, Sâo Tome, Principe, St. Helena, Mauritius, Reunion, Rodriguez, the Seychelles, Amirantes, New Caledonia and Tahiti. Attempted introductions on Madagascar and the Comoros failed (Peters, Check-list of the Birds of the World, Vol. 14, Mus. Comparative Zoology, Cambridge, Massachusetts, 1968).

The species has been feral in Manaus at least since 1967 (Sick, Bonn. Zool. Beitr. 19:298–306, 1968) and was first sighted in Belem in December of 1977 (Novaes, pers. comm.). The Manaus population comprises between 500 and 1000 birds (Oren and Smith, Acta Amazonica 8:699–701, 1978), whereas the Belem population probably numbers no more than a few dozen individuals. This waxbill has occurred in Rio de Janeiro perhaps since the late eighteenth century (Santos, Passaros do Brasil, 2nd ed., R. Briguiet, Rio de Janeiro, Brazil, 1948). From there it appeared in Sâo Paulo (1930) and subsequently in Vitoria (1940), Salvador (1953), Brasilia (1964), Maceio (1967), Curitiba (date unknown) and Porto Alegre (date unknown) (Pinto, Rev. Mus. Paulista 22:362, 1944; Sick 1968). The species is known to readily escape from standard-sized bird cages, and most subsequent populations probably started from escaped cage birds, although the population in Brasilia was established intentionally when over 100 individuals were released there (Sick 1968).

We have observed the waxbill in Manaus for more than a year, noting food plants, group size and relations with native species. This species disperses throughout the city and immediate environs during the day. At night birds concentrate in flocks of 50–200 individuals and roost in African elephant grass (*Pennisetum purpureum*) in a few sites in the city. During most of the year the waxbills form flocks of 2–20 to forage, feeding mostly between 06:00 and 09:00, and 16:00 and 18:00. This is the same pattern found by Skead (Ostrich, Suppl. 11:1–55, 1975) in Africa for the closely related Black-cheeked Waxbill (*E. erythronotos*). At the onset of the rainy season in late December and January, the flocks break up and the waxbills travel singly, in pairs, or sometimes in trios to forage. These months apparently encompass the peak of breeding, and flocks with many juveniles reform by mid-March.

The nest, constructed of panicles of Guinea grass (*Panicum maximum*), is in the form of a hollow ball with a short tubular entrance, as is the case in Africa (Chapin, Bull. Am. Mus. Nat. Hist. 75b:545–549, 1954). One nest was in an orange jasmin tree (*Murraya paniculata*, Rutaceae), and a second in an oiti tree (*Licania tomentosa*, Chrysobalanaceae)—both between 2.5 and 3.0 m from the ground.

Guinea grass, with seed heads available all year, was by far the most important food for *E. astrild*. Seeds of this grass are important in the diet in Africa also (Skead 1975). In fact, all grasses eaten by this waxbill in Manaus are species commonly found in Africa, and include the crabgrass *Digitaria horizontalis* (cosmopolitan in distribution), *Sporobolus indicus* (pantropical), *Echinochloa* sp. (pantropical) and *P. purpureum* (pantropical). The waxbills also feed on the amaranth *Amaranthus spinosus* (pantropical) and the sedge *Cyperus surinamensis* (Neotropical). Abundant native South American grasses, such as *Paspalum repens*, are ignored by the Common Waxbill.

The bird feeds on the seeds of *Panicum maximum* and *Pennisetum purpureum* by perching on the panicle and plucking seeds, whereas *D. horizontalis* panicles are jumped on, brought to the ground and stepped on so the waxbill can pluck the seeds. *C. surinamensis*, the only

food plant we recorded for the waxbill not found in Africa, is fed on in the same fashion as *D. horizontalis*.

Establishment of the Common Waxbill in Amazonia has been aided by the availability of introduced grasses, including *Panicum maximum* and *Pennisetum purpureum*. Some of these introduced grasses have long been established in South America (Parsons, Tübinger geografische Studien 34:141–153, 1970; J. Range Manage. 25:12–17, 1972) and are spreading with deforestation and other human disturbance. In addition, *Panicum maximum* is commonly planted as a pasture grass in Amazonia. The 15,000 km network of newly constructed roads in Amazonia could provide corridors along which African grasses grow and the waxbill might move to found new colonies. This, in conjunction with the waxbill's flocking behavior, could facilitate the further spread of this species in Amazonia.

Native Manaus finches, such as the Lesser Seedfinch (*Oryzoborus angolensis*), the Blue-black Grassquit (*Volatinia jacarina*), the Chestnut-bellied Seedeater (*Sporophila castaneiventris*) and the Yellow-browed Sparrow (*Ammodramus aurifrons*), frequently fed in close proximity to waxbills. These native birds eat native grass seeds in addition to the seeds of introduced plants, such that it seems unlikely that the Common Waxbill will displace any native species.—David C. Oren, *Dept. Biology, Harvard Univ., Cambridge, Massachusetts 02138 and Instituto Nacional de Pesquisas da Amazonia, Caixa Postal 478, 69.000 Manaus, Amazonias, Brazil* and Nigel J. H. Smith, *Instituto Nacional de Pesquisas da Amazonia, Caixa Postal 478, 69.000 Manaus, Amazonias, Brazil.* *Accepted 30 May 1980.*

Wilson Bull., 93(2), 1981, pp. 282–284

Distribution and reproductive success of Zone-tailed Hawks in west Texas.—The Zone-tailed Hawk (*Buteo albonatus*) occurs throughout the pine-oak belt of Mexico, including Baja California, and throughout Central America. In South America it also occurs widely but locally from Peru to Trinidad. In the United States the Zone-tailed Hawk breeds only locally in southern and central Arizona, southwestern New Mexico and west Texas (Brown and Amadon, Eagles, Hawks and Falcons of the World, Vol. 2, McGraw-Hill Co., New York, New York, 1968).

There are no historical data on the status or size of any Zone-tailed Hawk population. In 1976, Rich Glinski (pers. comm.) found 25 pairs of zone-tails in Arizona, but made no estimate of population size. In Texas, the species has nested recently in Taylor and Comal counties, in Brewster County in Big Bend National Park and in the Edwards Plateau area (Oberholser and Kincaid, The Bird Life of Texas, Vol. 1., Univ. Texas, Austin, Texas, 1974). Oberholser and Kincaid (1974) suggested that Texas populations have declined due to destruction of nesting habitat.

From 1 June–28 July 1975 and from 19 April–15 July 1976, we conducted a behavioral study and population survey of the Zone-tailed Hawk in west Texas. We surveyed the Chisos and Glass mountains and the Boquillas and Mariscal canyons of the Rio Grande River, all in Brewster County, and the Davis Mountains in Jeff Davis County. We did not survey the

entire Trans-Pecos, but checked the most likely breeding habitat for Zone-tailed Hawks: high mountains and lowland riparian cliffs. We surveyed 230 km² of the Davis Mountains, 195 km² of the Chisos Mountains, 5 km² of the Glass Mountains and 30 km of the Mariscal and Boquillas canyons.

The Davis Mountains reach an elevation of 2515 m, and zone-tail pairs nested on steep north-facing slopes among open stands of ponderosa pine (*Pinus ponderosa*). Nests were found between 1750 and 1900 m. The Chisos Mountains reach elevations of 2350 m; 1 zone-tail pair nested at 2000 m on a north-facing slope among a dense canopy of Emory oak (*Quercus emoryi*), grey oak (*Q. grisea*) and juniper (*Juniperus* spp.).

Both mountain ranges receive abundant rainfall during July, August and September. Annual rainfall is 46 cm (maximum) in the Davis Mountains (Ohlendorf, Wilson Bull. 86:357–373, 1974) and 64 cm (maximum) in the Chisos Mountains (Wauer, Southwestern Nat. 16:1–29, 1971).

Vegetation and weather conditions in Boquillas and Mariscal canyons contrast sharply with the high montane habitats. Desert shrubs predominated where zone-tail pairs nested in Boquillas Canyon on the upper-third of north-facing cliffs (averaging 65 m in height). Here, vegetation consisted mainly of creosote bush (*Larrea tridentata*), honey mesquite (*Prosopis glandulosa*), ocotillo (*Fouqueria splendens*) and lechuguilla (*Agave lechuguilla*). Average annual rainfall in the river canyons is ca. 25 cm. Temperatures for 5 months each year reach or exceed mean daily maximums of 38°C (Ohlendorf 1974).

All nesting territories used in 1975 were reused in 1976. We located 7 breeding pairs of Zone-tailed Hawks in 1975 and 9 in 1976 as follows: 1975—Davis (5) and Chisos (1) mountains, Boquillas Canyon (1); 1976—same as 1975 except 1 new nest each in the Davis Mountains and Boquillas Canyon.

In 1976, 5 Davis Mountain nests were within 1 m of the tops of 20–40 m ponderosa pines. The sixth nest was ca. 6 m from the top of a 40 m ponderosa pine. The Chisos Mountain nest was near the top of a 10 m Emory oak at the base of a 60 m cliff. All montane nests occurred near igneous rock faces 9–90 m high.

The Boquillas Canyon nests were on south-facing cliffs. We found 1 nest 5 m below the top of a 70 m cliff on a ledge about 3 m long and 1 m wide. We found another nest about 15 m below the top of a 60 m cliff in a hole in the cliff wall.

Although we never encountered Zone-tailed Hawks elsewhere, Deborah Davis (pers. comm.) observed a pair frequenting canyon cliffs south of the Davis Mountains at ca. 1500 m. We doubt that more than 15 pairs nested in the Trans-Pecos. In Arizona and New Mexico, however, these hawks apparently range widely over the desert slopes and up into the coniferous zone (Brown and Amadon 1968). Glinski (pers. comm.) indicates that in Arizona the Zone-tailed Hawk breeds in a wide range of habitats. In New Mexico, John Hubbard (in Porter and White, pp. 39–57 *in* Rept. Proc. World Conf. Birds of Prey, Vienna, Austria, R. D. Chancellor, ed., Int. Council Bird Preserv., 1975) found zone-tails nesting in pine forests, pine-oak, conifer and riparian woodlands.

In 1976, 4 of 9 nests fledged young compared to 6 of 7 nests in 1975 (Table 1). The 7 mountain pairs raised an average of 1.0 young in 1976, compared to 1.2 for the preceding season. Neither of the pairs at the Boquillas Canyon sites fledged any young in 1976, but 1 young fledged in 1975 from the single nest there.

During the second week of July 1977, Riley monitored the fledging success of the Chisos Mountain pair and 4 pairs in the Davis Mountains occupying the same sites as in 1976. At a nest approximately 100 m north of 2 previous nests, 2 young were near fledging on 8 July. Two other pairs, one at a new nest 200 m east of a nest-site on Sawtooth Mountain and one at the nest on Emory Peak, failed to hatch young. Nests at 2 sites near Timber Mountain in the Davis Mountains had apparently been abandoned.

Table 1

1975–1976 Reproductive Success of Zone-tailed Hawks in West Texas

	Nests	Eggs	Eggs hatched	Percent hatching success[a]	Young fledged	Percent nest success[b]
1975	7	14 (2)[c]	12 (1.7)[d]	86	8 (1.14)[e]	67
1976	9	18 (2)[c]	7 (0.7)[d]	39	7 (0.78)[e]	100

[a] Hatching success = no. of eggs hatched/no. of eggs laid.
[b] Nest success = no. of young fledged/no. of eggs hatched.
[c] Mean = no. of eggs/no. of nests.
[d] Mean = no. of eggs hatched/no. of nests.
[e] Mean = no. of young fledged/no. of nests.

We wish to acknowledge the support of the Chihuahuan Desert Research Institute which provided funds and equipment; this is Contribution No. 8 from that Institute. We would also like to thank Roger Krueger and James T. Harris for their indispensable field assistance.—Sumner W. Matteson, *Dept. Agricultural Journalism and Environmental Studies, Univ. Wisconsin, Madison, Wisconsin 53706* and John O. Riley, *Dept. Zoology, Univ. Wisconsin, Madison, Wisconsin 53706.* *Accepted 5 Apr. 1980.*

Wilson Bull., 93(2), 1981, pp. 284–285

Three Crested Eagle records for Guatemala.—The Crested Eagle (*Morphnus guianensis*) has not previously been reported for Guatemala (Brown and Amadon, Eagles, Hawks and Falcons of the World, McGraw-Hill Book Co., New York, New York, 1968:631). Russell (Ornithol. Monogr. 1, 1964) included no records for Belize, and Monroe (Ornithol. Monogr. 7, 1963:83) stated that the 2 Honduran records "are the northernmost records for the species." Peterson and Chalif (A Field Guide to Mexican Birds, Houghton Mifflin Co., Boston, Massachusetts, 1973) omitted this species from their field guide for Mexico, Guatemala, Belize and El Salvador. Herein we report a visual record (with photographic support) and 2 specimen records for Guatemala.

On the evening of 7 February 1978, while camped in a recently cleared area in the Petén area of east-central Guatemala, a medium-sized eagle passed directly over (25–35 m overhead) our camp and perched ca. 100 m away on a tall snag in the burned-over swamp. The bird remained ca. 5 min while we carefully observed it through 20X spotting scopes and photographed it with 300 and 350 mm lenses on 35 mm cameras. Thereafter, the eagle flew to another snag (ca. 150 m distant), remained ca. 2 min, then flew into the dense forest on a nearby mountain slope. After several minutes an eagle of the same species was again observed flying along the mountain slope, then into a tunnel-like opening in the dense forest canopy.

This observation took place near the southwest corner of Belize, less than 2 km west of the Petén highway (gravel) at a point ca. 48 km northwest of the Río Dulce crossing of Lago Izabal and 38 km south-southeast of the village of Poptún.

The following field characters were clearly noted, separating this bird from the somewhat similar Harpy Eagle (*Harpia harpyja*). The broadly barred primaries, secondaries and rectrices distinguished it from immature birds of both species. The bird did not have the blackish

breast band of an adult Harpy Eagle; rather, it had a light gray breast and very light belly characteristic of a normal phase adult Crested Eagle (Brown and Amadon 1968: plate 109). The general appearance of the bird was of a slender medium sized eagle rather than a stout large eagle as would be expected if the bird were a Harpy Eagle. Less clearly identified were the distinguishing traits of the crown. The bird, although carefully observed with its crown erect for several minutes, did not appear to have the double crest of *Harpia* but rather a single broad crest as in *Morphnus*.

Two final identifying traits were not clearly seen in the field but did show in photographs taken just as the bird left its nearer perch (photographs on file at the Institute for Raptor Studies). Brown and Amadon (1968: underwing plate 11) show the under wing coverts on the adult Harpy Eagle as heavily marked and, in general, as dark as the primaries and secondaries. The adult light phase Crested Eagle has nearly immaculate under wing coverts which contrast with the darker primaries and secondaries. The Harpy Eagle also has a light basal patch in its proximal primaries, a trait lacking in the Crested Eagle. In our photographs, the light basal patch characteristic of the Harpy Eagle is lacking and the under wing coverts appear unmarked. Both of these features are diagnostic of an adult Crested Eagle. In summary, all features observed on the bird lead to the conclusion that it was a light phase adult Crested Eagle.

On 8 February 1978, while visiting a small bakery in Flores, Guatemala (ca. 35 km southwest of the Mayan ruins at Tikal), we noticed that the whisk broom used to dust the counter had been made from the remiges and rectrices of a large, heavily barred raptor. The matron reported that the bird had been taken by hunters in the forest around Flores. We obtained a portion of the whisk broom, and subsequently compared these feathers with specimens at the American Museum of Natural History where they are now deposited (AMNH No. 812849). Our conclusion, later confirmed by John Bull, was that the feathers had come from an adult or subadult Crested Eagle.

An additional record came to our attention after our return to the United States (K. Kaufman and A. R. Phillips, pers. comm.). A Crested Eagle was recovered dead by Robert W. Dickerman (pers. comm.) 30–50 km east of Flores, Petén, Guatemala, on the road to Melchor de Mencos between 5 and 7 April 1966. The specimen (Royal Ontario Museum No. 115862), consists of a skeleton together with some remiges and rectrices, and was identified as an adult male (Jon C. Barlow, pers. comm.).

The previous northernmost and westernmost locations for this species were La Ceiba, Honduras, and San Pedro Sula, Honduras (Monroe 1963:83). All 3 records for Guatemala are north of La Ceiba, Honduras, and between 140 and 200 km west of San Pedro Sula, Honduras. These records extend the known range of the Crested Eagle over much of northern Guatemala. The close proximity of both the visual record and the 1966 specimen to the Belize border suggests that the bird may also occur there.—David H. Ellis, *Institute for Raptor Studies, Box 4420 OM Star Rt., Oracle Arizona 85623* and Wayne H. Whaley, *224 North 250 East, Orem, Utah 84057.* *Accepted 10 Apr. 1980.*

Wilson Bull., 93(2), 1981, pp. 286–300

ORNITHOLOGICAL LITERATURE

Population Ecology of Raptors. By Ian Newton. Buteo Books, Vermillion, South Dakota and T. & A. D. Poyser Ltd., Hertfordshire, England, 1979:399 pp., 32 black-and-white photographs, 50 figs., 68 tables at end of text, bibliography, index. $35.00.—This book was especially enjoyable to review because I associated with Dr. Newton as he gathered data for it. With great enthusiasm he took meticulous and voluminous notes during conversations on raptors. Authors of papers that caught his attention at meetings were interviewed, questioned and quizzed about their findings. I vividly remember how intense he became as he hurriedly jotted down and chronicled information in his notebook during a meeting we both attended in South Africa on African predatory birds. As a result of this zeal, there is some heretofore unpublished and considerable contemporary material in the book.

The author was among the last students of David Lack, by whom he was greatly influenced. Consequently, there is considerable reliance on food relationships throughout the text in explaining the data.

Although this book is published in the U.S. and Britain, the text is decidedly British in style, flavor, spelling and sentence structure. For example, "the last but one" for "next to last," "in fine weather," and "Gyr Falcon" instead of "Gyrfalcon" are typically used. In organization the text runs in a reasonable sequence. The sexes of raptors are discussed in chapter 1, followed by a series of chapters on breeding biology: chapter 3 breeding density, chapter 5 nest-sites, chapter 7 breeding strategies, chapter 10 fidelity to breeding areas, etc. This is followed by chapters on movements and mortality. Here, it seems, would have been a better place to put his chapter 2 on dispersion and chapter 4 on winter density. His final 5 chapters cover management oriented topics and contemporary problems such as chapters 14 and 15 on chemical pollutants and chapter 17 on breeding in captivity. He is extremely current on his treatment of these latter chapters, especially in light of the recent and often serious declines of raptors directly caused by humans and synthetic chemicals. The chapter on captive propagation evidences the recency of his data. Seemingly chapter 14 on DDT and other organo-chlorines, and chapter 15 on other pollutants and pesticides could have been combined and perhaps shortened, although only about 12% of the text was spent on the pollutant problem. The bibliography is excellent with over 800 citations and in itself is a good compendium and summary on raptor biology.

To develop support for some of the concepts, he uses carefully selected case history studies. For example, in a discussion of increasingly rare birds, he gives a blow-by-blow account of the studies on Lesser Spotted (*Aquila pomarina*) and Black (*A. verreauxi*) eagles wherein mortality of the young has been experimentally reduced. Rather than rely totally on work gathered from the literature, however, there are ideas seemingly expressed for the first time by Newton. For example, in his treatment of the reversed sexual dimorphism phenomenon in raptors, he offers a fresh new way to view the data (p. 23) and thus provides yet another explanation. I particularly appreciated Newton's insight in posing questions for fruitful future research with raptors. Many such questons, e.g., "Are populations of raptors so limited in winter as are some passerines that they cannot fully occupy the available breeding territories in spring and summer?" are, however, the very ones that are in need of work on most groups of birds. Some insight is suggested to that question by Newton's own research on the Sparrowhawk (*Accipiter nisus*) and he persuasively argues that raptor densities are directly correlated with food supply, which in turn is related to productivity of the land. This relationship appears to operate during all seasons.

The book is relatively error-free. I found only 3 typographical errors but they are minor, eg., Richlefs in place of Ricklefs (p. 126). In the text he gives the citation, Fyfe 1978 (p. 264)

while the closest to that in the literature cited is Fyfe 1976. The printing is nicely done, but in my copy p. 237 is poor because of heavy print, especially noticeable where double letters occur, as in egg. The citation of Belon (1555) (p. 199) on migration represents a fantastic bit of detective work in the literature.

There are some inconsistencies in the format of the text. Some of the chapters have discussions as special topics, and some do not. Rather than a summary at the end of each chapter, I would like to have seen a discussion of the material wherein Newton could have used his own insight and his keen inductive reasoning. Throughout the text he seems to resist speculating about concepts that are not clear and on some occasions, Newton even seems to apologize for having theorized or speculated.

I have mixed feelings about placing all the tables together in the back. When readers want to find a particular bit of data dealing with, for example, mortality from chapter 9, they must thumb through the graphs until they happen upon the data, unless they know the precise table number. I prefer the placement of tables in the chapter adjacent to the introduction and discussion of the data.

In his discussions of migration, there is a rather lengthy bit of data on North American migration, and I was surprised to see the omission of the very significant paper by Haugh (Search 2:1–60, 1972) that discusses the effects of the Great Lakes on migration. Newton even uses a figure to show migration along the Great Lakes (p. 197). It would also have been helpful to have the citation for Haldane's "incomplete data" methods as footnoted on p. 203.

Some observations that were generated during the reading of this book seem in order. Perhaps most salient is the virtual lack of data from the neotropics. It is not that Newton has neglected literature from there, but rather that there is little if any literature on neotropical raptor biology. It is one of the most diverse and interesting raptor faunas (primitive falconidae, the sub-buteos, etc.) and yet it remains so little known. There is a fruitful geographic area of research for the upcoming raptor biologists. It is clear from reading Newton that most of our knowledge about raptor biology pertains to holarctic areas, although considerable data are also available from Africa. Newton has been careful to explain particular methodologies used in the study of raptors. Few other books do this. He briefly explains how radio telemetry is being used and the mechanical basis of the techniques as pertains to raptors. He also cautions the reader (p. 231) to be careful in comparing data on ppm expressions of synthetic chemical residues in birds or their eggs by pointing out that some data are given as dry weight, some as wet weight and some as lipid weight. Each method gives a considerably different numerical value. It is unfortunate that his book came on the tails of Walter's book on the Eleonora's Falcon (*Falco eleonorae*) (1979, Univ. Chicago Press). Newton's discussion of the colonial species would have been more complete had he had access to Walter's book.

There is a wealth of data on breeding biology that can be implied by a use of morphological expressions of birds. These data are largely ignored. For example, further support for the concept of fidelity to breeding areas can come from the study of geographic variation, locations of recognizable demes, etc., as well as from actual banding data. Many raptors are noted for the occurrence of recognizable demes based on external morphology (presumably this will be corroborated by blood protein morphology once that technique has been sufficiently tried on birds). Biologically this recognition is perceptible when members of a given deme return to the general region to breed and selection pressure intensity for a given trait far exceeds the rate of dispersal to another area or immigration rate of new genetic expressions. Such morphological traits are potent evidence of the lack of panmixis on a level larger than the local population or deme.

The overall wealth of material and Newton's manner of presenting it make this a valuable book for those who not only want to learn about raptors but also for those who are interested

in the biology of bird populations in general. I hope that the price is not too restrictive for those young biologists who can profit most from such a book.—Clayton M. White.

The Foraging Behavior of Mountain Bluebirds With Emphasis on Sexual Foraging Differences. By Harry W. Power. Ornithological Monographs No. 28, American Ornithologists' Union, 1980:ix + 72 pp. $8.50.—This is a very stimulating monograph, which is a tactful way of saying that it makes many debatable points. Power first reviews the theory of how sexual differences in foraging might come about. He then demonstrates that female Mountain Bluebirds (*Sialia currucoides*) tend to use more energetically expensive methods of foraging than males, and recalls his theoretical review in order to understand why this difference exists. He sets up a series of experiments adjusting brood sizes, removing parents and manipulating habitats, all designed to discriminate between the theoretical alternatives. He concludes that none of the alternatives are well supported, but leans toward a "division of labor" interpretation. He does discover, however, that both males and females have a common tendency to use more expensive foraging tactics when their work load increases, and that females are more inclined to make this increase than males, at least when the work load increase is in terms of young to feed per adult.

The detailed biology in the midst of theoretical boldness and experimental ingenuity in the field makes this work a major contribution to modern ornithology. I make this claim in spite of the fact that I would have interpreted the data rather differently.

Power presents himself as an evolutionary biologist, and writes with a measure of arrogant dogmatism. But the writing is so clear and Power himself so thoughtful of his readers, that one is willing to overlook his confidence in his own reasoning (and in the naïveté of those he disagrees with). The net effect is exciting, and I suspect that Mountain Bluebirds are destined to become a "classic" or textbook species for discussions of avian foraging strategies.—Stephen D. Fretwell.

Population Dynamics: The 20th Symposium of the British Ecological Society. By R. M. Anderson, B. D. Turner and L. R. Taylor (eds.). Blackwell Scientific Publications, Oxford, England; distributed in the U.S.A. by Halstead Press of John Wiley & Sons, Inc., New York, New York, 1979:434 pp. $69.95.—An exciting component of ecology as a discipline is the constant challenge provided by theoretical and empirical advances. The breadth and vitality of recent advances in population ecology are well represented in this volume. A total of 18 chapters with 27 authors surveys a variety of subjects: the influence of behavior and genetics as determinants of population dynamics; the importance of mosaics in determining population size in space and time; the role of life history strategies in determining population characteristics; the existence of multiple stable states in ecological communities; and the influence of trophic structure on community dynamics. The foundations of many of the dogmas of the past two decades are weakened by these presentations.

In the only strictly avian chapter, Diamond examines the now familiar question of randomness vs competition in the evolution of island faunas—neither extreme represents truth. Avian examples are involved in two other chapters. Cowie and Krebs use foraging patterns in insects and birds to explore optimal foraging in patchy environments. They, like other authors, emphasize the importance of integrating the behavior (Taylor and Taylor) and genetics (Berry, Law) of individuals in understanding population dynamics. Both Berry and Law note that life histories—rates of reproduction and risks of death—are evolving under forces imposed by prevailing environments. Since they may be doing so at a pace that is within the time scale of ecological studies, they cannot be ignored. In an analysis of spruce budworm populations, Peterman, Clark and Holling conclude that birds may play a primary

role in determining the lower stable population attractor and thus, equilibrium densities, of spruce budworm.

Although only one chapter concentrates on birds, there is much to be learned here by ornithologists willing to make the effort. Many of the chapters are dominated by mathematical models. Typically, these are coupled with analysis of the details of an intriguing biological system. The merger of theory with observations often yields insights that either alone is incapable of producing. Overall, cogent arguments are presented for avoidance of simplistic models dependent on average populations and their rates of change. More realistic models will deal with the spatial and temporal variability in populations.

Many of the chapters in this volume are integrative combinations of observation, theory and application. There are few typographical errors, and extensive cross referencing among chapters attests to the efforts of the editors to increase the value of the volume. Speaking of value, its $69.95 price tag will encourage use of library copies. It is worth the effort to search out a copy and read.—James R. Karr.

The Island Waterfowl. By Milton W. Weller. Iowa State University Press, Ames, Iowa, 1980:x + 121 pp., 27 numbered figs., 12 tables. $10.95.—The island waterfowl this book treats are the distinctive species or races of ducks and geese (Anatidae) that have evolved in isolation following earlier colonization of oceanic islands or archipelagos, largely in the tropics and the southern oceans. The lure of remote islands and scarce animal forms is probably sufficient to ensure that this book will find readers, despite the rather high price of such a slim volume. Nevertheless, my initial scepticism as to the need for such a book remained after 2 readings. Weller had already published the results of his field studies on 5 island groups—Tierra del Fuego, Falklands, South Georgia, New Zealand and Auckland Islands—and his wish to synthesize the results of those and other work on island waterfowl could have been done as effectively in a review article for a journal. The objectives of the book, which emerge only gradually, seem to be to define the characteristics of successful island waterfowl and to predict whether vacant niches exist for future colonizations of specific archipelagos, while encouraging further research on these birds to fill gaps in existing knowledge. The book is thus addressed to fellow-scientists rather than to the general public.

One may carp at the questionable need for this book, but its standards of scholarship are as high as one would expect from a scientist of Weller's calibre. The individual forms are described and located geographically, the factors influencing colonization of islands and the subsequent responses to constraints posed by island situations are described, and the development of the waterfowl faunas of the island groups Weller had studied is analysed. A brief chapter considers conservation measures for scarce species. There are 8½ pages of references (in fine print) and an index. The text is easily read and adequately proofed (I noted only 2 or 3 typos), and the diagrams and illustrations are clear and informative. My chief difficulty with the make-up of the book was its lack of an introduction, the first chapter plunging straight into lists and descriptions of island forms. The Preface covers some of the introductory material needed, but how many readers will think to read the Preface first?

Weller repeatedly emphasizes the need for adaptability in successful colonizers, most of which stemmed from the dabbling ducks (*Anas*). Adaptations to islands include the ability to use marine and shoreline environments for part or all of the year, resistance to cold on the part of the young and even more so for the adults, and so on. He seems not to have remarked that such characteristics exist in several of the largely north temperate and subarctic species of diving ducks (tribes Somateriini and Mergini), which thus may be preadapted for colonization of cold south temperate or subantarctic islands. The extinct Auckland Merganser (*Mergus australis*), and the steamer ducks (*Tachyeres*), which latter resemble and fill

the niches occupied by the eiders (*Somateria*) in the north, presumably have evolved from representatives of such northern groups. The same adaptations allow those northern diving ducks to winter farther north, so trans-equatorial migrations that could lead to colonization of southern islands are not regular among those groups; those individuals that do reach remote islands may be as promising colonists as are *Anas* ducks.

The discussion of habitat use and resource partitioning might be read to advantage by waterfowl biologists concerned with carrying capacity and introductions, though these, as well as biology of island waterfowl, need more quantitative data. Study of the island microcosm also reminds one of its vulnerability, and the extent to which man has affected the numbers and distribution of continental waterfowl in the past and present. Some species of waterfowl, as well as other game birds, were nearly eliminated from eastern North America by unregulated hunting in the 1800's, and when populations began to recover they found eastern habitats transformed from forest to largely open landscapes. Thus, we have "prairie" ducks moving in to breed all over northeast America, even into artificial impoundments that simulate prairie sloughs in largely forested regions. If Weller's book stimulates more thought and research on such topics, its spinoff value will go a long way to justify its publication.—Anthony J. Erskine.

Woodland Grouse Symposium. By T. W. I. Lovel (ed.). World Pheasant Association, Daws Hall, Lamarsh, Bures, Suffolk, United Kingdom, 1979:180 pp., 3 photographs, 18 maps, 40 text figs. and 32 tables. £8.—This report of a symposium held in Scotland in December 1978 contains papers and notes on 2 species of capercaillie, the Black, Hazel, Ruffed, Blue and Spruce grouse, and briefly Willow and Rock ptarmigan. Participants came from most of the northern countries of Europe, USSR, Iran, China, Japan, Canada and U.S. Sessions were devoted to the present status of woodland grouse species in 7 countries; the ecology of woodland grouse (7 papers), field and analytical techniques (3 papers), behavior of woodland grouse (3 papers) and management of woodland grouse (5 papers).

Marcström briefly reviews the literature on population fluctuations of European woodland grouse. Synchrony in population changes of different species within an area, and variability in periodicities, are features of the Scandinavian stocks.

Reports from Norway, Sweden, Finland, Denmark and Poland suggest a general decline in numbers of most grouse species, which are attributed to changes in forest exploitation practices, habitat loss, changes in weather patterns and acid rain pollution.

In France, Capercaillie (*Tetrao urogallus*) survive in 4 isolated mountain chains. They are widespread and hunted only in the Pyrenees. A relic population of Black Grouse (*Lyrurus tetrix*) remains on lowland moorland in the Ardennes. In alpine habitat, the species is still found in 9 departments adjacent to Switzerland and Italy. They were never found in the Pyrenees. Ellison reviews his work on hunted and unhunted Black Grouse populations in the French Alps. Fall hunting removed about 57% of the males. An unbalanced sex ratio and few old males does not seem to have affected productivity.

Tso-Hsin Cheng outlines the status of grouse in China. Hazel Grouse (*Tetrastes bonasia*) are found in the Northern Region and a closely related species (*Tetrastes sewerzowi*), in the Southwest Region. Black Grouse of 3 subspecies are found in extreme northeastern and northwestern China, and the Black-billed Capercaillie (*Tetrao parvirostris*) in the northern part of the Great Khingan Mountains, and perhaps the northern part of the Altai Range.

The Black-billed Capercaillie is confined to upland forest dominated by larch (*Larix gmelini*). Food is largely shoots and buds of white birch and larch. In summer they eat blueberries, huckleberries (*Vaccinium* sp.) and bird cherries (*Craetagus* sp.). Spring display begins in late March and mating from mid-April to early May.

Andreev reports on the reproductive behavior of the Black-billed Capercaillie in Siberia.

His description suggests some differences from the displays of the Chinese birds. In China, display is largely arboreal and starts at 2:00–3:00, lek behavior has not been recorded. In Siberia, males display in groups of 6–10 on the ground, usually on snow. They perform all night, starting at sunset, with a lull around midnight. Their lek activity may persist for an extraordinarily long period, exceeding 12 h.

In China, the birds migrate to river valleys for the winter. Their numbers may be declining because of changes in habitat due to intense land use. Tso-Hsin Cheng's account of the Black Grouse includes the old folk-lore story of males spitting saliva on the ground and females following to pick it up.

The winter ecology of woodland grouse is discussed in papers by Andreev on bioenergetics, Pulliainen on composition and nutrient content of fall and winter food of Capercaillie, and Glutz von Blotzheim and students on the winter behavior and food of Black Grouse and food of the Hazel Grouse.

Angelstam reports on reproductive success and survival of Black Grouse in relation to population fluctuations of small mammals. Data from 1977 and 1978 suggest that survival of eggs, chicks and adults were higher when small mammals were abundant. Little information is given on methods used to judge density of small mammals and no data on the species present, only the bank vole (*Clethrionomys glareolus*) is mentioned.

The only paper on North American woodland grouse is given by Bendell and Zwickel. North American biologists will be familiar with the variety of papers by these authors, in the case on Bendell, extending for over 25 years. Their paper describes the characteristics of Spruce (*Canachites canadensis*), Blue (*Dendragapus obscurus*) and Ruffed (*Bonasa umbellus*) grouse. They briefly review what is known about population regulation, causes of levels of density, management and distribution of these species.

Porkert, in an important paper, discusses the influence of human factors on the populations of tetraonids in north-eastern Bohemia and northern Moravia. In addition to the often recognized factors of human disturbance and habitat changes, there is also the impact of air pollution and acid rain.

Isolated and now endangered populations of Capercaillie, Black Grouse and Hazel Hens live in the Orlické hory Mountains, which rise to 1115 m. The prevailing winds that flow over the Bohemian industrial basin impinge at right angles to this range. The foothills are narrow and do not intercept the precipitation carried by air masses from the west. The geological structure is poorly buffered schist. At 870 m precipitation averages 126.5 cm per annum and is 2–3 times higher than in the neighboring foothills. Fog and ice storms are frequent. The average annual value of acid precipitation is estimated at about 4.2. Spring thaw is accompanied by a sharp drop in pH amounting to about 1 unit.

The most heavily polluted sites are those under the crowns of old trees, mainly spruce, under which there was almost complete destruction of *Vaccinium myrtillus* in the winter of 1975–76, which had a particularly acute episode of pollution. In open sites, *V. myrtillus* were less heavily damaged and regenerated better. This species is an important grouse food, particularly for Capercaillie.

Decline of Capercaillie and Black Grouse numbers might not be due entirely to air pollution because other factors are also influential. However, these species have also declined rapidly in the east-Sudeten area. There, and in the Krkonoše and Beskydy Mountains, changes in forest management were introduced much later than in the Orlické hory Mountains, but the decline occurred at the same time as the development of heavy chemical industry and construction of large thermal power plants.

Recommendations for harvest management of Capercaillie in Scotland are made by Moss, Weir and Jones. After consideration of a variety of field studies, they conclude that under the shooting methods (driving) employed in open natural forest, 16% would be a safe harvest.

In the areas studied about 15% of the birds seen were killed on the first shoot of the year. This safe harvest rate is much lower than for other forest species of grouse for which data are available.

In planted forest, densities of Capercaillie were similar to those recorded in Finland and were lighter than in natural forests. The proposals made by Bancik for the conservation of Capercaillie in Slovakia, in contrast, seem naive and contain many of the outworn panaceas of an earlier age. There is no presentation and analysis of field data, only proposals to regulate certain logging practices to specific times of the year to minimize disturbance to the birds, but nothing about regulating logging so as to create or maintain suitable habitat.

Potts, in an all too brief paper, stresses the value of modeling as an aid to studies of game bird populations, using his experience with the Grey Partridge (*Perdix perdix*) as an example.

This symposium gives a good overview of the work on tetraonids in Europe and Asia. Over most of Europe, Capercaillie and Black Grouse are declining. The view of the participants is that in the future, priority should be given to intensive studies of population dynamics.—Harry G. Lumsden.

Proceedings of the Workshop Management of Southern Forests for Nongame Birds. Richard M. DeGraff (Tech. Coord.). U.S.D.A. For. Serv. Gen. Tech. Rept. SE-14., Southeastern Forest Experiment Station, Asheville, North Carolina, 1978:176 pp., 53 figs., 29 tables. No price given.—This is another in the Forest Service sponsored series on the regional management of nongame birds. The term "nongame" is well defined, easy to understand and has management meaning, but as of late has fallen from grace with certain editors and its use in print may be diminishing. Nevertheless, almost every paper in this workshop uses the term to denote non-"harvested" wildlife species. Although concern for nongame wildlife is not new, only recently has there been any action taken. The main reason for this has been lack of funding, both in the failure of conservation groups to raise enough money and the reluctance of state and federal agencies to use "hunting and fishing" funds to look at songbirds, as well as the absence of any key legislation to provide monies for nongame research. Michael Zagata of the National Audubon Society outlines the history of such problems in the keynote address. In sum, he cites the rise in interest in nongame management and documents recent legislation such as the Missouri nongame act designed to benefit nongame wildlife, which raised about $26 million in 1978. He concludes by calling for increased amounts of funding at the federal level, and justifies this call by documenting the current widespread public interest in nongame wildlife.

The workshop is divided into 4 sections: Forest Ecosystem Structure and Function and Effects on Birdlife, with the keynote address and 2 additional papers; Effects of Management Practices on Nongame Birds, with 6 papers; Specialized Bird Habitats and Management, with 4 papers; and a concluding paper on future research plans. Like all workshops there are many "nonpapers" in this one and many of the papers could have been written for any of the other regional workshops by simply changing the names of the bird species and leaving most of the text unchanged. Moreover, there is much interpaper redundancy in these particular workshop proceedings. However, some of the papers are of great interest and practical use. Chandler Robbins provides a very useful paper on census techniques for forest birds, a topic on which there is probably none better qualified to speak than he. He compares spot mapping (or plot census), transect methods, point counts (the IPA method) and the Breeding Bird Survey (BBS), as well as covering banding, nest finding, tape recordings and techniques for winter and other nonbreeding season surveys. He concludes that, although all methods have some level of imprecision, the spot-mapping method is generally best; but other techniques such as transect lines are most effective when many plots are being compared. Another interesting paper is by Noon and Able, "A Comparison of Avian Community Structure in

the Northern and Southern Appalachian Mountains." Not only is the methodology in this paper of interest, but useful data and interesting results are provided. They compare bird data from Mount Mansfield in Vermont with the Great Smoky Mountains, plotting birds on elevational and other environmental gradients. It is unfortunate that they do not have data for the central Appalachians, such as West Virginia, to add to their comparisions.

This workshop, like most others, is loaded with material that apparently could not make it in a refereed journal. Yet if one is successful at sifting the wheat from the chaff, new information and knowledge can be gleaned from its pages.—Robert C. Whitmore.

Audubon Birds of America. Introduction and Commentaries by Roger Tory Peterson. Crown Publishers, Inc., New York, New York, 1979 (? no date) :160 pp., 72 full-page plates (color), 30 much-reduced illustrations (color) on 4 pp. $17.95. Audubon. A Biography. By John Chancellor. The Viking Press, New York, New York, 1978:224 pp., 116 illustrations (16 color). $17.95. The Double Elephant Folio. The Story of Audubon's Birds of America. By Waldemar Fries. American Library Association, Chicago, Illinois, 1973: xxii + 501 pp., frontispiece (color), 45 test-figs. $45.00.—John James Audubon (1785–1851) was unusual in various ways, as in being an ornithologist who made money. Indeed, he has continued to do so for those with the enterprise to market his evidently inexhaustible appeal. The rather large number of these now includes Roger Tory Peterson, another ornithologist of financial acumen, and Crown Publishers, Inc.

If there is additional reason for the present book, it would appear to be whatever interest attaches to Peterson's choice of "102 favorite" (a phrase from the dust jacket) Audubon pictures. Some years ago I ventured (Scientific American 216:156, 1967) to nominate a minimum of 17, all but 2 of which have made it onto Peterson's list. So much for taste. This is not a work of criticism or interpretation. The brief biographical introduction provides nothing new, but perpetuates the myth laid to rest, one would have thought, by Alice Ford (John James Audubon, Univ. Oklahoma Press, Norman, Oklahoma, 1964) that Audubon studied under Jaques Louis David. The often amusing commentary which accompanies the pictures is about birds, not art, and has no clear raison d'être except to fill space. On p. 44, discussing the immature Bald Eagle (*Haliaeetus leucocephalus*) (the "Bird of Washington," as Audubon called it), Peterson perpetrates a howler in saying that Florida has more of this species than any other state, while on p. 54, discussing the adult, he correctly notes that Alaska has more than all other states combined. The plates are well reproduced, but the color is more intense than in any elephant "folio" that I have seen. They provide an instructive sampling, however, for any one without ready access to Audubon's birds. The legends of the Leach's Petrel and Trumpeter Swan are transposed on p. 159.

Biographies of Audubon are numerous and continue to appear along with the pictures. Chancellor's is refreshing in presenting a rarely unbiased picture of Audubon's complex and not altogether adorable personality. The highly readable but nonetheless scholarly text, with numerous figures of contempory scenes and events, does a good job of placing Audubon in context. There are occasional perplexities, as on p. 172, where Chancellor observes that the California Condor was "the subject of an Audubon controversy" not otherwise mentioned, nor known to me. Could he mean the one over the sense of smell in Turkey Vultures? Anent this, on p. 41 he has Audubon contending that the latter have a well developed sense of smell (as K. Stager has shown that they do), while on p. 187 he has Audubon contending (as he did) that they do not. These small matters notwithstanding, this is probably the best brief biography of Audubon to date.

The chief of Audubon's several works, the so-called double elephant "folio" (actually broadsheet) stands as the most ambitious effort at bookmaking in history, and is exceeded in physical size only by the Napoleonic atlases of Egypt. It is itself the subject of an ex-

haustive monograph by Waldemar Fries, the third of the items in hand. This, which shows every evidence of relentless and careful scholarship, is an indispensable reference for the serious student of Audubon iana, containing not only the details of the undertaking: history, subscribers, costs, sets and censuses thereof, but also appendices covering related editions, reproductions, prospectuses, fates of copper plates, chronology of engraving variants, and related miscellany.

This notice will complete the record in drawing the last work to the attention of Wilson Bulletin readers. That it did not appear as a contemporary review owes to one of the present writer's occasional lapses into terminal procrastination. Having now partially made amends, I shall cease avoiding review editor Raikow at professional meetings.—Robert M. Mengel.

The Warblers of America. Edited by Ludlow Griscom and Alexander Sprunt, Jr. Revised and updated by Edgar M. Reilly, Jr. Illus. by John Henry Dick. Doubleday and Co., Inc., Garden City, New York, 1979:xv + 302 pp., 35 color plates. $19.95.—The first edition of this book (1957) was apparently a hastily gathered and loosely organized work assembled as a frame of reference for John Henry Dick's color plates. Several chapters treated general matters such as parulid taxonomy, methods of study and song. Then followed brief accounts of the plumage and aspects of the life history of all species covered by the A.O.U. Check-list. Next, a series of chapters dealt with the warblers of geographic regions lying outside the contiguous United States. Dick's plates depicted adults and, in many cases, sub-adults of all parulid species recognized in 1957. Finally, brief appendices gave further attention to systematics and described certain migration routes. The manuscript of that edition had been read by various reviewers and authorities; their comments and additions, instead of being integrated into the text, were incorporated as bracketed annotations.

Although this second edition is said to be both revised and updated, nothing has been done to integrate the original hodgepodge. The revisions are exceedingly limited and deal principally with taxonomic changes, and the updating consequently ignores much of the work of the last 20 years. I see no justification for republishing the book. Compared to other recent volumes that summarize knowledge of entire familes, e.g., Nelson on the sulids or Hancock and Elliott on the herons, it falls woefully short.

Two early chapters on song still describe vocalizations in the old-fashioned way, reporting such qualities as hoarseness, wiriness, etc., and endeavoring to spell songs out in the letters of the alphabet. This was acceptable in 1957, but it is not acceptable today, when even field guides present sound spectrograms. (W. W. H. Gunn, co-author of one of the song chapters, informs me he was given no opportunity to revise his chapter and indeed was not told that it was to be republished.) Ludlow Griscom's chapter entitled "The techniques of warbler study" is particularly unfortunate. The novice consulting it will almost surely conclude that the study of warblers consists largely of learning what they look like, counting them and recording locations and dates of observation. Nor will he or she be encouraged to attempt even these limited tasks after reading Griscom's statement that expertise calls for talents "completely beyond the natural capacity of most individuals." Those with sufficient hardihood to continue in the face of such odds are instructed in heavily pontifical language which too often has little substance. "I list below the various stages by which expertness in warbler study may be attained: I. Clearly the first step is to acquire an awareness of warblers."

Most of the species accounts are by Sprunt, who is inclined to tell the reader less about a species than about how he feels toward it. Some warblers are clowns, other sprites or animated jewels; they are petite, dainty, breathtaking, enchanting; their haunting melodies are as played on the pipes of Pan. Sprunt at times reports as fact points for which it is hard to imagine the supporting data. Can he have had evidence for Orange-crowned Warblers

(*Vermivora celata*) that "even normal migrational hazards [do] not seem . . . to affect them as much as many other species," and what other species had he in mind? On the other hand, when facts are available, he sometimes appears either to ignore them or to write so loosely as to mislead. For example, he states that Prairie Warblers (*Dendroica discolor*) in the north are victimized by cowbirds (*Molothrus* sp.) and that in the south, where cowbirds are absent, racoons and snakes sometimes take a toll, as though these threats to nest success replace each other. Those species reports contributed by other authors, e.g., Van Tyne on Kirtland's Warbler (*D. kirtlandii*), are often more factual and informative.

Considering that the book has color plates of all species and that even the most casually interested person can be expected to have a field guide, a great deal of space in the species narratives could have been saved had the rather superficial plumage descriptions been eliminated. Range maps (breeding ranges only) are presented with each account and are said in the preface to have been revised for this edition. I feel qualified to comment on only 1 map: that for the Prairie Warbler was not accurate in 1957, and the revised version has not corrected the errors.

The most useful chapters in the book are those summarizing the warblers of Mexico, Central America, the West Indies, Panama and South America. I found Bond's contribution on Central America and Eisenmann's on Panama particularly well organized and helpful. In contrast, the chapters on Alaska, British Columbia, the prairie provinces of Canada and eastern Canada overlap a good deal. And since they deal with the species covered by the A.O.U. Check-list, they contain much material that either duplicates the species accounts or that probably would have been more effectively presented in good, factual species accounts. This is not the fault of the contributors of these chapters, who wrote to fulfill their assignments from the editors of the first edition.

If the foregoing is largely critical of what the book originally contained, I find even more fault with the editorial policy that preserved the earlier work at the expense of most of the recent (and not so recent) studies of warblers. Omitted, for example, are findings of Mayfield on Kirtland's Warbler, of M. Ficken on the American Redstart (*Setophaga ruticilla*), of Foster on the Orange-crowned Warbler, of various students on the Blue- (*V. pinus*) and Golden-winged (*V. chrysoptera*) warblers and their hybrids, and of work on the Prairie Warbler. Meanley's study of Swainson's Warbler (*Limnothlypis swainsonii*) is mentioned only in a bracketed 1-sentence interpolation. Other warbler research of importance is also ignored, e.g., MacArthur on population ecology, Morse on foraging and on song, Mengel on speciation, the Fickens on comparative ethology. Van Tyne refers to banding and some of the results produced by that method of studying Kirtland's Warbler, but I recall no other reference to banding; the significant population data that it has generated are not discussed anywhere.

I am not competent to evaluate Dick's plates. Those interested in that feature of the book may want to refer to George Sutton's critical analysis in his review of the first edition (Auk 75:226–228, 1958).—Val Nolan, Jr.

To A Young Bird Artist: Letters from Louis Agassiz Fuertes to George Miksch Sutton. Commentary by George Miksch Sutton. Univ. Oklahoma Press, Norman, Oklahoma, 1979:147 pp., 4 color plates, 5 details of Fuertes' letters. $9.95.—A tragic accident in August of 1927 cut short the very abundant career of perhaps the greatest bird painter of all time—Louis Agassiz Fuertes. There is a resultant sense of loss not only for the man, but also for the work never produced due to his untimely death. Consequently, any new work dealing with Fuertes merits celebration and a book such as this, which deals so intimately with Fuertes as an individual, as a painter and as the genius he was, deserves special attention.

This book consists of the letters Louis Agassiz Fuertes wrote to George Miksch Sutton between the years of 1915 and 1927, interspersed with Sutton's commentary on those letters, on Fuertes and on their collective influence on him. The correspondence took place while Fuertes was at the height of his career and while Sutton was struggling through the early stages of his development. The correspondence ended with Fuertes' death. Through the letters and narrative, the reader gains insight into the lives of both Fuertes and Sutton and their special relationship. But this book offers more than that. If the reader will endeavor to truly understand the principles presented, he will have gained an awareness and knowledge enabling him to better understand not only Fuertes and Sutton, but all of bird art. In this sense, the book is a primer on bird art which is valuable not just to those interested in painting but to anyone who is interested in birds—for birds and bird art are inseparable. Interest in birds is highly dependent upon our visual sense and it is in the visual sense that this book has its one fault. For a book dealing with bird art and bird artists, it does not seem to fully realize its potential in terms of illustration. But this fault is acceptable in that the book is intended to give the reader an understanding of bird art and this it does successfully.—Larry Barth.

Parrots, Their Care and Breeding. By Rosemary Low. Blandford Press Ltd., Poole, Dorset, United Kingdom. Distributed in the U.S.A. by Sterling Publishing, Inc., New York, New York, 1980:654 pp., 91 color photos. $55.00.—Until recently, parrot aviculture has been mainly restricted to the maintenance of non-breeding exhibit collections, or household pets. The parrot was regarded as a household fixture, like the lap dog, or the fern. Since it was soon discovered to be noisy, messy and sometimes destructive, the bird was probably kept in some out-of-the-way corner of the house, permanently confined to a small cage, and fed an unvarying diet of hard seed. Similarly, with few exceptions, zoos maintained collections to satisfy the curiosity of the public, and made no effort to provide conditions that might promote breeding. During the last 50 years the increasing awareness of ecology, and the application of scientific techniques to animal care has caused a change in approach. Parrots are now more often provided with diets suited to their specific needs, and circumstances that promote a better psychological outlook. Increasing import restrictions and depletion of wild populations have stimulated more and more parrot fanciers to become parrot breeders.

Whether one is interested in the proper maintenance of a single pet, or in a large-scale breeding program, this book will, by itself, supply the necessary information. Low has produced the most comprehensive and scientifically based work on parrot-keeping to date. The book is largely a compilation of her own and other aviculturists' experiences, tempered with biological explanations. The result is a large amount of information presented in a very readable manner.

The book is divided into 2 parts. In part one, topics pertinent to the care of any type of parrot are considered. The problems of choosing, housing and feeding are discussed in detail. A constant theme of these chapters is that prospective parrot-keepers be practical in their choice of birds. The means and life-style of the keepers must be matched with the needs of their parrots. For example, Low would abhor the thought of a tame Blue and Yellow Macaw (*Ara ararauna*) living in a small apartment whose owner was away at work 10 h a day.

Specific directions for aviary construction are given, along with suggestions for accommodations in colder climates. In a section on aviary management, both daily and long-range tasks, as well as emergency measures, are discussed. One of the strongest points of the book is the detailed coverage of feeding requirements. Commonly encountered seeds, vegetables and fruits are analyzed for food value and vitamin content. Low dispenses with the commonly-held and harmful notions that: (1) all parrots, other than lories and lorikeets, eat about the same thing—hard seeds of one size or another, and (2) parrot diets should be conservative

and unvaried. Most species of the genus *Amazona*, she feels, could do very well on the diet of their keepers.

The chapters related to breeding give excellent, up-to-date summaries on all aspects of the subject. Low's discussion of pair-bonding points out a much neglected area in parrot-keeping. Some species bond, and some do not, and an awareness of this is essential for proper aviary management, as well as understanding the behavior of a tame pet. Methods of sexing, appropriate nesting materials and special dietary needs of breeding parrots are discussed. Low advocates hand-rearing not just as an emergency measure, or a means of creating pets, but because she has found that it increases breeding success. Guidelines for construction of incubators and preparation of formulae are provided.

Although there is no doubt that Low's primary interest is in breeding parrots, the chapter on maintaining pets is exceptional. The over-riding point here is that pet parrots should be regarded as amusing and time-consuming companions, not merely as mimics or household adornments. Accordingly, as many suggestions are given for their psychological as for their physical well-being.

Part one is concluded with a chapter on sick birds. Anyone who has been subjected to a sick parrot can understand why this is a relatively neglected area in aviculture. Sick birds deteriorate very rapidly, and even if proper diagnosis can be made, treatment is often uncertain and more traumatic than the ailment. Low, nevertheless, competently summarizes what is known about sick parrots in general, along with methods of prevention, diagnosis and treatment of specific illnesses. Much of the information is certainly based on her own extensive experience.

The remainder of the book, part two, is devoted to the care and breeding of particular species. All genera and most species of parrots encountered in aviculture are discussed individually. Each chapter covers a general category of birds such as Australian parakeets, macaws, or hanging parrots, based on traditional taxonomic opinions. Following general comments on each group, there is a subsection devoted to each genus and species that includes range, habitat, description, avicultural history, feeding, accommodation and breeding in sufficient detail to prepare any prospective aviculturist for maintenance of the bird. Comments on natural history are brief, the reader being referred elsewhere for this matter. Although the descriptions are excellent, the book would be enhanced by more color plates. Those plates that are included are of good quality, and seem to have been selected to represent both typical and aberrant examples of the various parrot groups.

In addition to her obvious delight in aviculture, Rosemary Low has an objective that is both openly expressed and implied throughout her book—the elimination of the necessity of importing birds from their natural habitats. Aviculture can still be a hobby, but it should be refined so that it is possible to acquire any bird, whether for breeding or as a pet, from domestic stocks. Low has certainly done her part toward making this a reality.

I recommend this book highly for anyone interested in parrots, and for general, as well as, scientific libraries. The price is a bit high, but the thorough and up-to-date coverage makes acquisition of other books on parrot aviculture unnecessary.—Susan L. Berman.

Lovebirds and Their Color Mutations. By Jim Hayward. Blandford Press, Ltd., Poole, Dorset, United Kingdom. Distributed in the U.S.A. by Sterling Publishing, Inc., New York, New York, 1980:108 pp., 32 color photos, numerous black-and-white photos and drawings. $14.95.—This pleasant little book covers everything one needs to know about breeding lovebirds (*Agapornis* spp.), from the maintainance of a simple aviary to the production of the rare and fancy color mutations. Because of their beauty, small size and willingness to breed in captivity, lovebirds have long been popular among aviculturists. The increasing variety of color mutations in recent years has been an added incentive for breeding them.

In spite of these features, lovebirds have never attained the avicultural status of the Budgerigar, probably because of their shortcomings as pets. Even tame lovebirds can be pugnacious toward their keepers at times, and their nesting habits cause them to be destructive when left free and unsupervised in a household. Accordingly, the book contains no charming anecdotes about favorite pets. Hayward discusses only topics related to their breeding.

The style is chatty and agreeable if one can overlook the occasional misuse of words. Hayward's approach is that of a hobbyist, not a scientist, emphasizing the "how-to," but seldom the "why."

There are 4 chapters on subjects of a general nature. Aviary construction and management is covered briefly, and adds nothing not found in most standard parrot books. The chapter on feeding, although brief, is of value in being based on Hayward's extensive experience as a lovebird breeder. The best source of information on feeding any bird is one who has bred them, as most birds won't breed unless they are maintained on an appropriate diet.

Likewise, Hayward's experience is evident in the 2 chapters on problems related to breeding and health. In a concise but thorough manner, he summarizes the common difficulties, their prevention and treatment. Brand names of medication and precise dosages are given. Hayward is particularly helpful in providing directions for administering the appropriate treatment. All too often in avicultural literature one is not told how to get that antibiotic or worming medication into the bird. Hayward accomplishes this verbally and with the aid of photographs.

The major portion of the book is devoted to descriptions of the various lovebird species and their color mutations. The reader is prepared for the emphasis on the latter area by a short and very elementary chapter on bird genetics. Following this, a description of each species, along with its distribution and avicultural status, is given. Hayward comments on specific food and housing problems, and advises which species are more likely to breed in cold, damp climates. For species commonly yielding color mutations, Hayward provides "recipes" for producing them—a handy guide for the beginner. The color plates are of good quality and exhibit the variety and beauty of these little parrots.

Although the book is unscientific in its approach, and would not be helpful for one interested in the behavior or natural history of lovebirds, I think anyone inclined to breed them would find this a useful manual.—Susan L. Berman.

Arctic Summer: Birds in North Norway. By Richard Vaughan. Anthony Nelson Ltd., Salop, England, 1979:152 pp., 7 color plates, 96 black-and-white plates with captions, 2 maps, 1 table. £6.25. Available in the U.S.A. from Buteo Books, P.O. Box 481, Vermillion, South Dakota 57069.—This interesting little book describes the author's 38-day bird-watching and photography adventure on the Varanger Peninsula of Norway's most northerly county, Finnmark. The book is written as a naturalist's account and travelog of ornithological events in Finnmark during the exceptionally dry spring and early summer (6 June–19 July) of 1972. The author's photographs are excellent and comprise over half the book. The narrative is personal and describes the immediate events surrounding his trip; however, Vaughan, an historian at England's Hull University, also contributes a number of interesting historical anecdotes, and provides insights into the life histories of many birds in the area. The annotated "Systematic list of the birds of the Varanger Peninsula" at the end of the book is current up to the end of 1978.

In some parts, complicated sentences and overpunctuation make for slow reading. However, the assets of the book outweight its minor liabilities. The annotated list, along with the names of local ornithologists and descriptions of the best camping locations, make Arctic Summer a valuable campanion for bird enthusiasts visiting northern Norway.—Stephen R. Johnson.

Iceland Summer: Adventures of a Bird Painter. By George Miksch Sutton. Univ. Oklahoma Press, Norman, Oklahoma, 1980 (1961):253 pp., 7 color plates, numerous monochrome sketches and photgraphs. $5.95.—This is a reprinting in paper covers of a book first published in 1961. An account of the author's travels in search of birdlife, it received the John Burroughs Medal in 1962.—R.J.R.

The Complete Birds of the World. By Michael Walters. David & Charles, Inc., North Pomfret, Vermont, 1980:340 pp. $35.50.—This book consists of an annotated list of all extant and recently extinct species of birds of the world. They are listed by family (but not by order), and the basic classification followed is that of the Peters Check-List, modified in a few cases by reference to more recent works. Although it was published in 1980, work on the manuscript ceased in 1977, so some recent references, including Vol. 8 and the revised Vol. 1 of Peters, were not consulted. For each species there are a few sentences summarizing data on distribution, habitat, food, nest-site, clutch-size, sexes that incubate and period of incubation, and fledging period. This is a reference work that aims for breadth of coverage rather than depth. Misspellings are numerous.

Of what use is such a book? The intended purpose is not explained. It could be helpful if one wanted to known the taxonomic composition of a particular family, or for a very sketchy outline of its biological features. The book could have been made much more useful by providing an index to genera, species and English common names, instead of only to families. One could then have used it, for instance, to identify unfamilar forms encountered in reading. As it stands, however, to do this one must first know the family and then search for the form in question. In a large family this can be very tedious. In short, this volume represents a good idea whose potential was not fully developed.—Robert J. Raikow.

A Manual for Bird Watching in the Americas. By Donald S. Heintzelman. Universe Books, New York, New York, 1979:255 pp., 8 color plates, numerous black-and-white photos. $17.95.—In this book Heintzelman combines a potpourri of practical information on bird-watching with extensive discussions of birding throughout the Americas based on his own travels. The first part deals with equipment and literature, especially field guides, and includes names and addresses of birding organizations. There are also chapters on group activities such as Christmas bird counts and Big Day counts, nest record programs, feeders and the like. Much of this will be familiar to experienced birders, but beginners should find some useful information. The rest of the book gives accounts of birding trips in various areas of North and South America, as well as Arctic and Antarctic regions. There are also chapters on watching particular groups of birds, such as waterfowl, hawks, owls, shorebirds and warblers. The color photos are of good quality, but many of the black-and-white photos lack sharpness and contrast.—R.J.R.

Call Collect, Ask for Birdman. By James M. Vardaman. St. Martin's Press, New York, New York, 1980:256 pp., 8 pp. of black-and-white photos, 2 appendices, charts, sighting ledger, map. $10.95.—In 1 year, 1979, the author attempted to see 700 of the 800-plus North American bird species. This book recounts that effort, for which he spent $44,000, traveled 161,000 miles and fell 1 bird short of his goal. The book is not about birds, but rather about the strategy and logistics of finding them. Vardaman's approach to bird-watching brings out one aspect of "ABA-ism" at its worst—the appreciation of birds only as an offshoot in the quest for a longer life-list (year-list, in this case). He includes copious details about the "super-birders" who found most of the birds for him, but practically no information is given about key field marks, plumages, or behavior of the birds themselves. Other organized

attempts to set high-count birding records have generated money for conservation causes. Vardaman apparently made no effort to grace his well-publicized "Big Year" by soliciting such donations. Buyers of this book are reimbursing the author's forestry consulting firm for the cost of the Big Year attempt. Birders may find interesting the locations of hard-to-find species; biologists will find the book of no value.—Mark Holmgren.

The Birds of Brevard County. By Allan D. Cruickshank, edited by Helen G. Cruickshank. Florida Press, Inc., Orlando, Florida, 1980? (undated):xv + 204 pp., 1 map, 1 black-and-white photo, hard cover. $12.00.—This is a collection of records of birds occurring in Brevard County, Florida, as compiled from 1950–1974 by the late Allan D. Cruickshank, with contributions by other observers, and added records (1974–1978) by Robert D. Barber. The book includes a map of Brevard County, an introduction by Helen G. Cruickshank and a brief biography of the author. The bulk of the book is devoted to the records, which include the following information, where appropriate, for each species: common and scientific names, arrival dates, dates of maximum abundance, winter visitants, departure dates, breeding status, egg dates and status as a resident or migrant. This work should be a useful aid to birders on the east coast of Florida.—R.J.R.

Bird Finding in Tennessee. By Michael Lee Bierly. Published by and available from the author at 3825 Bedford Ave., Nashville, Tennessee 37215, 1980:255 pp., numerous maps, paper cover. $8.00 postpaid.—One hundred-twelve birding areas in Tennessee are discussed with remarks on habitat, travel information and expected species. Several large-scale and numerous local maps pinpoint birding areas. In addition, there are brief comments on status and abundance of the 342 species recorded from the state, a list of birders in various areas who can be contacted for local information and a compilation of local chapters of the Tennessee Ornithological Society.—R.J.R.

Welcome the Birds to Your Home. By Jane and Will Curtis. The Stephen Greene Press, Brattleboro, Vermont, 1980:154 pp., paper cover. $5.95.—Chatty advice on attracting and studying birds, and a bit of painless natural science are the features of this little book aimed at the beginning amateur ornithologist.—R.J.R.

This issue of *The Wilson Bulletin* was published on 20 August 1981.

The Wilson Bulletin

Editor Jon C. Barlow

Department of Ornithology
Royal Ontario Museum
100 Queen's Park
Toronto, Ontario, Canada M5S 2C6

Assistant Editor Margaret L. May

Senior Editorial Assistants Gary Bortolotti
Nancy Flood

Editorial Assistants Keith L. Bildstein
C. Davison Ankney
Richard R. Snell
James D. Rising

Review Editor Robert Raikow
Department of Biological Sciences
University of Pittsburgh
Pittsburgh, PA 15260

Color Plate Editor William A. Lunk
865 North Wagner Road
Ann Arbor, MI 48103

Suggestions to Authors

See Wilson Bulletin 91:366, 1979 for more detailed "Suggestions to Authors." Manuscripts intended for publication in *The Wilson Bulletin* should be submitted in triplicate, neatly typewritten, double-spaced, with at least 3 cm margins, and on one side only of good quality white paper. Do not submit xerographic copies that are made on slick, heavy paper. Tables should be typed on separate sheets, and should be narrow and deep rather than wide and shallow. Follow the AOU Check-list (Fifth Edition, 1957) and the 32nd Supplement (Auk, 90:411–419, 1973), insofar as scientific names of U.S. and Canadian birds are concerned. Summaries of major papers should be brief but quotable. Where fewer than 5 papers are cited, the citations may be included in the text. All citations in "General Notes" should be included in the text. Follow carefully the style used in this issue in listing the literature cited; otherwise, follow the "CBE Style Manual" (1972, AIBS). Photographs for illustrations should have good contrast and be on gloss paper. Submit prints unmounted and attach to each a brief but adequate legend. Do not write heavily on the backs of photographs. Diagrams and line drawings should be in black ink and their lettering large enough to permit reduction. Original figures or photographs submitted must be smaller than 22 × 28 cm. Alterations in copy after the type has been set must be charged to the author.

Notice of Change of Address

If your address changes, notify the Society immediately. Send your complete new address to Ornithological Societies of North America, % Sandra L. L. Gaunt, Box 21160, Columbus, Ohio 43221.

The permanent mailing address of the Wilson Ornithological Society is: c/o The Museum of Zoology, The University of Michigan, Ann Arbor, Michigan 48109. Persons having business with any of the officers may address them at their various addresses given on the back of the front cover, and all matters pertaining to the Bulletin should be sent directly to the Editor.

Membership Inquiries

Membership inquiries should be sent to Dr. Robert C. Whitmore, Division of Forestry, West Virginia University, Morgantown, West Virginia 26506.

CONTENTS

THE RUFOUS-FACED CRAKE (*LATERALLUS XENOPTERUS*) AND ITS PARAGUAYAN CONGENERS
Robert W. Storer 137

RESOURCE USE STRATEGIES OF WADING BIRDS ---- *James A. Kushlan* 145

AGE RATIOS AND THEIR POSSIBLE USE IN DETERMINING AUTUMN ROUTES OF PASSERINE MIGRANTS ---- *C. John Ralph* 164

WEATHER, MIGRATION AND AUTUMN BIRD KILLS AT A NORTH FLORIDA TV TOWER
Robert L. Crawford 189

CLIMATIC INFLUENCES ON PRODUCTIVITY IN THE HOUSE SPARROW ---- *W. Bruce McGillivray* 196

CANADA GOOSE BROOD BEHAVIOR AND SURVIVAL ESTIMATES AT CREX MEADOWS, WISCONSIN
Michael C. Zicus 207

BREEDING BIRD POPULATIONS IN THE GREAT SMOKY MOUNTAINS, TENNESSEE AND NORTH CAROLINA ---- *S. Charles Kendeigh and Ben J. Fawver* 218

NEST-SITE SELECTION AMONG ADÉLIE, CHINSTRAP AND GENTOO PENGUINS IN MIXED SPECIES ROOKERIES ---- *Nicholas J. Volkman and Wayne Trivelpiece* 243

COWBIRD PARASITISM AND EVOLUTION OF ANTI-PARASITE STRATEGIES IN THE YELLOW WARBLER ---- *Karen L. Clark and Raleigh J. Robertson* 249

INTERACTIVE BEHAVIOR AMONG BALD EAGLES WINTERING IN NORTH-CENTRAL MISSOURI
Curtice R. Griffin 259

PRESIDENT'S MESSAGE ---- 264

GENERAL NOTES

INTERSPECIFIC SONG MIMESIS BY A LINCOLN SPARROW
Luis F. Baptista, Martin L. Morton and Maria E. Pereyra 265

NOTES ON PURPLE GALLINULES IN COLOMBIAN RICEFIELDS ---- *Wallace D. McKay* 267

AGONISTIC BEHAVIOR OF THE WHITE-BREASTED NUTHATCH ---- *Lawrence Kilham* 271

EVASIVE BEHAVIOR OF AMERICAN COOTS TO KLEPTOPARASITISM BY WATERFOWL
Mark R. Ryan 274

ADDITIONAL EVIDENCE OF EGG-MOVING BEHAVIOR BY FEMALE GADWALLS
Robert J. Blohm 276

MALLARD USING MOVING VEHICLES FOR PREDATOR AVOIDANCE
Bruce C. Thompson and James E. Tabor 277

OCHRACEOUS WREN FAILS TO RESPOND TO MOBBING CALLS IN AN HETEROSPECIFIC FLOCK
William H. Buskirk 278

FISH ATTACK ON BLACK GUILLEMOT AND COMMON EIDER IN MAINE *Thomas W. French* 279

CROWS STEAL GOLF BALLS IN BANGLADESH ---- *Richard M. Poché* 280

NOTES ON THE STATUS OF THE COMMON AFRICAN WAXBILL IN AMAZONIA
David C. Oren and Nigel J. H. Smith 281

DISTRIBUTION AND REPRODUCTIVE SUCCESS OF ZONE-TAILED HAWKS IN WEST TEXAS
Sumner W. Matteson and John O. Riley 282

THREE CRESTED EAGLE RECORDS FOR GUATEMALA
David H. Ellis and Wayne H. Whaley 284

ORNITHOLOGICAL LITERATURE ---- 286

WIL
8424
.a

COMP. ZOO
LIBRARY
NOV 16 1981
HARVARD
UNIVERSITY

The Wilson Bulletin

PUBLISHED BY THE WILSON ORNITHOLOGICAL SOCIETY

VOL. 93, NO. 3 SEPTEMBER 1981 PAGES 301–456

THE WILSON ORNITHOLOGICAL SOCIETY

FOUNDED DECEMBER 3, 1888

Named after ALEXANDER WILSON, the first American Ornithologist.

President—Abbot S. Gaunt, Department of Zoology, Ohio State University, Columbus, Ohio 43210.

First Vice-President—Jerome A. Jackson, Department of Biological Sciences, P.O. Drawer Z, Mississippi State University, Mississippi State, Mississippi 39762.

Second Vice-President—Clait E. Braun, Wildlife Research Center, 317 West Prospect St., Fort Collins, Colorado 80526

Editor—Jon C. Barlow, Department of Ornithology, Royal Ontario Museum, 100 Queen's Park, Toronto, Ontario, Canada M5S 2C6.

Secretary—Curtis S. Adkisson, Department of Biology, Virginia Polytechnic Institute and State University, Blacksburg, Virginia 24061.

Treasurer—Robert D. Burns, Department of Biology, Kenyon College, Gambier, Ohio 43022.

Elected Council Members—Richard C. Banks (term expires 1982); Mary H. Clench (term expires 1983); Helen Lapham (term expires 1984).

Membership dues per calendar year are: Active, $16.00; Student, $14.00; Sustaining, $25.00; Life memberships $250 (payable in four installments).

THE WILSON BULLETIN is sent to all members not in arrears for dues.

THE JOSSELYN VAN TYNE MEMORIAL LIBRARY

The Josselyn Van Tyne Memorial Library of the Wilson Ornithological Society, housed in the University of Michigan Museum of Zoology, was established in concurrence with the University of Michigan in 1930. Until 1947 the Library was maintained entirely by gifts and bequests of books, reprints, and ornithological magazines from members and friends of the Society. Now two members have generously established a fund for the purchase of new books; members and friends are invited to maintain the fund by regular contribution, thus making available to all Society members the more important new books on ornithology and related subjects. The fund will be administered by the Library Committee, which will be happy to receive suggestions on the choice of new books to be added to the Library. William A. Lunk, University Museums, University of Michigan, is Chairman of the Committee. The Library currently receives 195 periodicals as gifts and in exchange for *The Wilson Bulletin*. With the usual exception of rare books, any item in the Library may be borrowed by members of the Society and will be sent prepaid (by the University of Michigan) to any address in the United States, its possessions, or Canada. Return postage is paid by the borrower. Inquiries and requests by borrowers, as well as gifts of books, pamphlets, reprints, and magazines, should be addressed to: The Josselyn Van Tyne Memorial Library, University of Michigan Museum of Zoology, Ann Arbor, Michigan 48109. Contributions to the New Book Fund should be sent to the Treasurer (small sums in stamps are acceptable). A complete index of the Library's holdings was printed in the September 1952 issue of *The Wilson Bulletin* and newly acquired books are listed periodically. A list of currently received periodicals was published in the December 1978 issue.

THE WILSON BULLETIN
(ISSN 0043-5643)

The official organ of the Wilson Ornithological Society, published quarterly, in March, June, September, and December. The subscription price, both in the United States and elsewhere, is $20.00 per year. Single copies, $4.00. Subscriptions, changes of address and claims for undelivered copies should be sent to the Treasurer. Most back issues of the *Bulletin* are available and may be ordered from the Treasurer. Special prices will be quoted for quantity orders.

All articles and communications for publications, books and publications for reviews should be addressed to the Editor. Exchanges should be addressed to The Joselyn Van Tyne Memorial Library, Museum of Zoology, Ann Arbor, Michigan 48109. Known office of publication: Department of Zoology, Ohio State University, 1827 Neil Avenue, Columbus, Ohio 43210.

Second class postage paid at Columbus, Ohio and at additional mailing office.

© Copyright 1981 by the Wilson Ornithological Society

Printed by Allen Press, Inc., Lawrence, Kansas 66044, U.S.A.

Mainland Rufous-backed Robin *(Turdus rufo-palliatus, above)* and Grayson's Robin *(T. graysoni, below).* Painting by Anne Pulich.

THE WILSON BULLETIN

A QUARTERLY MAGAZINE OF ORNITHOLOGY

Published by the Wilson Ornithological Society

VOL. 93, NO. 3 SEPTEMBER 1981 PAGES 301–456

Wilson Bull., 93(3), 1981, pp. 301–309

SUBSPECIES VS FORGOTTEN SPECIES: THE CASE OF GRAYSON'S ROBIN *(TURDUS GRAYSONI)*

ALLAN R. PHILLIPS

Anyone reading ornithological books and papers of the past 30–50 years must be confused about subspecies. On one side is the tendency to reduce all possible species to subspecies, as long as they are thought to be allopatric. Biological similarities or differences tend to be ignored, especially because we know so little about them in many tropical species. Once pronounced a subspecies, a bird is promptly forgotten by most ornithologists, field guides, bird watchers, etc.

On the other side, paralleling the anti-evolutionists of 100 years ago, we have the anti-"subspecies concept" drive, denying the reality of subspecies. In the recent summary of avian biology, edited by Farner and King (1971), we read that "many [unnamed] avian systematists are now convinced that the subspecies category is unsatisfactory if not worthless"; while a long chapter on "Geographic Variation" (Farner and King 1971:76–92) mentions none of the classic striking cases, e.g., *Motacilla* spp. wagtails or, in North America, *Otus* spp. owls (Marshall 1967), *Junco* spp., and various other emberizine sparrows, including *Pipilo* spp. towhees (Phillips 1959).

If there is actually a subspecies concept, it is that such very unlike birds interbreed more or less freely to form a single unit, the biological species. In other genera, on the other hand, much subtler differences separate full biological species, as in *Empidonax* spp. flycatchers and *Cisticola* spp. and *Phylloscopus* spp. warblers. In the tropics, there may well be a number of similar cases where our fragmentary data have led to hasty reduction of allopatric, or supposedly allopatric, species to subspecies. Let us examine one such case, that of Grayson's Robin (*Turdus graysoni*) of Nayarit, western México.

This case is somewhat parallel to that of The Frantzius' (=Ruddy-capped) Nightingale-Thrush (*Catharus frantzii*); both *T. graysoni* and *C. frantzii* were swept into oblivion by Hellmayr (1934). Whereas some authors never accepted Hellmayr's dictum that the differences between *C. frantzii* and the Russet Nightingale-Thrush (*C. occidentalis*) were mere individual variations (see references in Phillips 1969), *Turdus graysoni* disappeared completely except as a subspecies in technical papers (omitted from field guides, as are most subspecies). Consequently, we still lack biological evidence, so ably presented for *Catharus* spp. by Rowley and Orr (1964) and Raitt and Hardy (1970). One present objective is to awaken interest in the biology of the 2 *Turdus*.

In recent years, ornithologists and bird-watching tours have flocked to San Blas, Nayarit, by the hundreds. Any robins seen were perforce listed as Rufous-backed (*T. rufo-palliatus*) or White-throated robins (*T. phaeopygus* of Phillips, unpubl. [=*assimilis*]). If a *T. graysoni* was seen, readers of Blake (1953:423) or perhaps Edwards (1972) might call it a female *T. rufo-palliatus*; others would have to force it into one of the above two forms or into the Clay-colored Robin (*T. grayi*), which does not really occur within hundreds of kilometers of Nayarit. This cost little strain; for now, as Robert O. Paxton (1979), president of the Linnaean Society of New York, wrote in reviewing recent bird books in a popular magazine: "No one 'sees' a bird in totality, feather by feather. One sees parts of it, and the mind fills in the rest by guesswork or (if one knows birds already) by memory." Thus, sightings of robins in coastal Nayarit are as worthless scientifically as are those of the much more similar kingbirds (*Tyrannus*) of the Caribbean slope of México and Guatemala (Traylor 1979).

Grayson's Robin was considered an insular form, limited to the Tres Marías Islands off Nayarit, until Nelson (1899) reported one taken at Santiago Ixcuintla, on the opposite mainland. Hellmayr (1934:356, footnote) questioned this, writing that *graysoni* "is merely a pale, large-billed race of the mainland bird [*rufo-palliatus*]. Certain individuals of the latter in worn breeding plumage closely approach it in coloration, and it is no doubt on such a specimen that Nelson's record of *T. r. graysoni* from Santiago, Nayarit, was based." He gave no measurements.

Clearly, Hellmayr (1934) should have examined Nelson's bird. Not only is it very dull, but it is larger than *rufo-palliatus*; my minimum measurements may be compared in Table 1. While most of these are possible for either form, the tarsus agrees only with *graysoni*, supporting Nelson's (1899) identification. The longer tarsus of *graysoni*, overlooked by Hellmayr (1934), had been carefully explained by Ridgway (1907:106–107), who gave it as 33–35 mm (vs 30.5–34 mm in mainland males, 30.5–32 mm in females). He gave the exposed culmen as 22–23 mm (vs 19–22.5 mm),

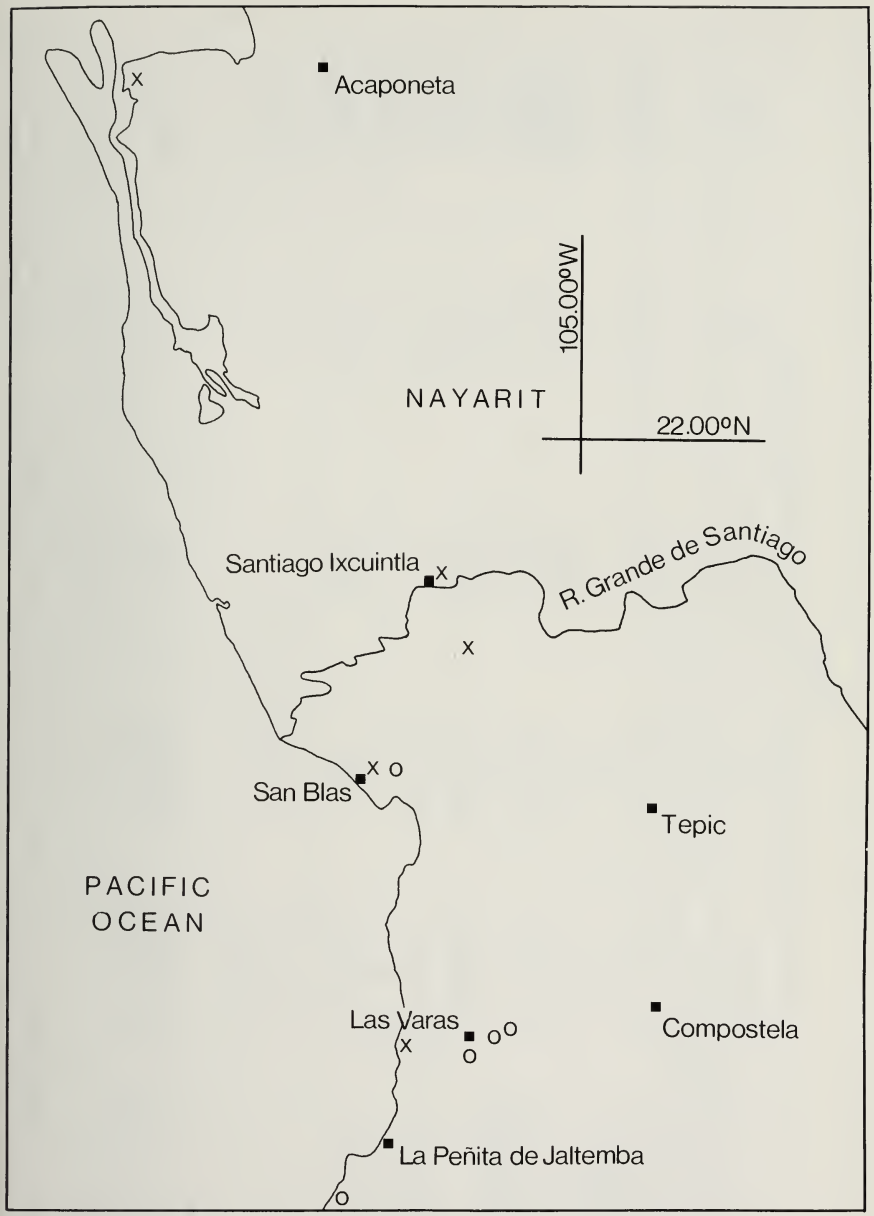


FIG. 1. Records of Grayson's (crosses) and White-throated robins (circles) in the lowlands of western Nayarit. Upland records are not mapped, but upland cities (Tepic, Compostela) are shown for orientation. (Upper limit of mapping records is 500 m elev.) Rufous-backed Robins probably occur throughout the lowlands, and are not mapped.

Table 1

Measurements of *Turdus* spp., from Nayarit (Except as Noted)

	Wing (chord) (mm)	Tail (mm)	Exposed culmen[a] (mm)	Bill[b] (mm)	Tarsus (mm)
T. graysoni					
Tres Marías Is., ♂♂ (Grant 1965) (N = 20–22)	121.9–132.7 ($\bar{x}$ = 127.17)	95.4–107.9 ($\bar{x}$ = 102.49)	22–23 ($\bar{x}$ = 22.6)	13.3–16.2 ($\bar{x}$ = 15.18)	33.0–36.3 ($\bar{x}$ = 34.8)
Sauta, ♂ (Grant 1965)	123.6	99.6	—	13.9	31.6
Tres Marías Is., ♀♀ (Grant 1965) (N = 34–39)	118.5–131.2 ($\bar{x}$ = 124.97)	84.4–105.7 ($\bar{x}$ = 99.6)	22–22.5 ($\bar{x}$ = 22.3)	14.2–17.4 ($\bar{x}$ = 15.42)	31.9–38.1 ($\bar{x}$ = 34.67)
Novilleros, ♀ (McKitrick)	121	89	25.6	14.9	35.1
Santiago, ♀	119.9[+]	96.7[+]	20.5[+?]	14.4	34[+?]
Chacala and Sauta, ♀♀ (Grant 1965) (N = 3)	118.9–123.4 ($\bar{x}$ = 121.17)	94.9–100.3 ($\bar{x}$ = 97.43)	—	13.8–15.2 ($\bar{x}$ = 14.53)	32.2–34.5 ($\bar{x}$ = 33.17)
San Blas, ♀ (MVZ only)	121, 126[−?]	95, 95	20.5, 21	15.6, 15.8	32.7, 32.8; or 33.9, 34.5
Total mainland, ♀♀ (N = 7)	118.9–123.4, 126[−?] ($\bar{x}$ = 121.4)	89–100.3 ($\bar{x}$ = 95.4)	20.5–21, 25.6	13.8–15.8 ($\bar{x}$ = 14.9)	32.2–35.1 ($\bar{x}$ = 33.4[+?])
T. rufo-palliatus					
Mainland, ♂♂ (Grant 1965) (N = 30–32)	117.3–128.2 ($\bar{x}$ = 123.19)	91.8–105.4 ($\bar{x}$ = 99.29)	19–22.5 ($\bar{x}$ = 20.5)	12.2–14.6 ($\bar{x}$ = 13.26)	29.4–33.8 ($\bar{x}$ = 31.48)
San Blas, ♂♂ (N = 7)	—	—	17.2±–19.2±, 21	12.2–14, 14.8	29.7–32.7, 33.5

Table 1
Continued

	Wing (chord) (mm)	Tail (mm)	Exposed culmen[a] (mm)	Bill[b] (mm)	Tarsus (mm)
Guerrero (and SW Oaxaca), ARP[c], ♂♂ (N = 24)	—	—	16.7, 17.5–19.5, 20.3	—	29.7–33, 33.6
Mainland ♀♀ (Grant 1965) (N = 20–22)	115.7–123.4 ($\bar{x}$ = 120.42)	90.4–101.9 ($\bar{x}$ = 95.85)	19–22.5 ($\bar{x}$ = 20.7)	12.5–14.7 ($\bar{x}$ = 13.80)	29.3–33 ($\bar{x}$ = 31.19)
San Blas, ♀♀ (N = 3)	—	—	18.7–19.1	13.5–14.2	30.5–32.2± (or 32.45)
Guerrero (and to SW Oaxaca, Colima), ♀♀ ARP[c] (N = 14)	—	—	17.3–19.5	—	29–31.8, 32.8

[a] Exposed culmen from Ridgway (1907), for first (main) series of each sex; his *rufo-palliatus* not from Nayarit.
[b] From just inside anterior edge of nostril.
[c] All ARP are in author's private collection and were taken from October–January except 2 ♂♂, 1 on 4 March and on 8 July (the longest exposed culmen—worn).

[although, as has sometimes been noted, linear extreme measurements may give but a poor idea of differences in bill size (easily distorted by slight differences in calipers or in techniques; cf. for example, the careful analyses of Knox 1976).] The accompanying plate (frontispiece) of *graysoni* was painted directly from Nelson's specimen, which is worn but not excessively so.

Nevertheless, Hellmayr's (1934) classification has been followed ever since, even by Miller et al. (1957), with Nelson's specimen right before one of the co-authors (Friedmann). Grant (1965) identified 4 other mainland specimens as *graysoni*, also from coastal Nayarit (Sauta and Chacala); but he considered all these to be stragglers of the island subspecies. He reported no intermediates, nor have I identified any.

Grant (1965:33) also cast doubt on Ridgway's (1907) reported differences in dorsal colors, writing that mainland females, on the back, "are indistinguishable from all island birds" and males only "slightly more rufous." But Ridgway (1907:105) seems to me quite correct in calling mainland females "often not distinguishable, but usually [?] very slightly duller in color" than mainland males, which are usually strikingly reddish-backed, quite unlike *graysoni*. There is a certain range of variation in both sexes; I suspect that adult males are more consistently bright (reddish) dorsally than other age/sex classes. Nevertheless, all these overlap greatly, and all *rufo-palliatus* seen by me show at least some cinnamon-rufous or chestnut dorsally. In dull extremes, this may show only on the scapulars.

I have, however, found 4 more *T. graysoni* from the mainland coast (San Blas and west of Acaponeta). That all nine are stragglers from the islands is hardly believable, for they show a definite distribution. The only somewhat parallel case, where the island race has been taken repeatedly on and near the mainland, is in the *Parula* warblers. Here it seems clear that the "Tres Marías form" (*P. americana* [=*pitiayumi*] *insularis*) completely replaces the migratory mainland Tropical Parula (*P. americana* [= *pitiayumi*] *pulchra*) in the breeding season in the coastal mangroves and islands; the 2 races are allopatric in summer. *Turdus*, on the other hand, is not regularly migratory. *T. rufo-palliatus* occurs, and appears to be irregularly common, at most or all of the mainland points where *T. graysoni* has been taken. If it alone were of normal occurrence, it should far outnumber *graysoni* in random collecting. But in fact, along the immediate coast, the difference is not very great (9 *rufo-palliatus* to 6 *graysoni*; Table 2). Furthermore, collecting is not all random; collectors may prefer pretty or distinctive specimens. When I first visited Nayarit, in the 1950's, I wanted chiefly distinctive representatives of the species: either clearly white-throated or definitely reddish birds. If in fact I ever saw any *T. graysoni*, I did not want them, being quite unaware of the problems.

TABLE 2
SPECIMENS OF *TURDUS* EXAMINED FROM LOWLAND NAYARIT[a]

T. phaeopygus (=*assimilis*)	
15 km E, San Blas, 10 Feb. 1956	1 ♀, LSU[b]
8 km E, 6 km S, San Blas, 15 Apr. 1965	1 ♂, UNM
10 km E, Las Varas, 26 Mar. 1941	1, RTM
15 road km E to Las Varas area, 12–17 Nov. 1852, 17 June 1970	1 ♂, 2 ♀♀, ARP, MEXU
Lo de Marcos (S side), 5 Apr. 1955	2 ♂♂, 2 ♀♀, ARP
Total, 12 Nov.–17 Jun.	4 ♂♂, 5 ♀♀ & 1?
T. graysoni	
Novilleros, 4 Feb. 1966	1 ♀ im., ARIZ
Sauta, 12 May 1940, 25 Apr. 1946	1 ♂, 1 ♀, RTM
Santiago Ixcuintla, 20 June 1897	1 ♀, US
San Blas, 20, 25 Mar. 1948	3 ♀♀, MVZ RTM
Chacala, 15–21, Mar. 1941	2 ♀♀, RTM
Total, 4 Feb.–20 June	1 ♂, 8 ♀♀
T. rufo-palliatus	
8 km S of Acaponeta	6, RTM
Sauta, 1–17 May	2 ♂♂, 2 ♀♀, RTM
Santiago Ixcuintla, 1889	1 ♂, BM
San Blas and vicinity, 10–19 Oct., 27 Dec., 4 May (1889, 1925, 1955, 1963)	5 ♂♂, 3 ♀♀, BM, CAS, CM, MVZ
15 km E, San Blas, 8–23 Feb.	3 ♂♂, 1 ♀, LSU
15 km E to Las Varas area,	5, RTM, ARP
11 km W, Mazatán, E Las Varas (lowlands?), 26 Dec.	1 ♀, DEL
Chacala, 9 Mar. 1941	1 ♀, RTM
Total	11 ♂♂, 8 ♀♀ & 11 (+?)

[a] West of Tepic area, excluding extreme south.
[b] See acknowledgments for abbreviations; ARP, author's private collection.

If so many *graysoni* were conspecific stragglers, we should expect an influence of their characters in coastal *rufo-palliatus*. But neither Grant (1965) nor I found clear evidence of this, though a few specimens (Moore Lab. of Zoology) approach *graysoni* slightly in color, being duller than average *rufo-palliatus*. A regular migration from and to the islands is most unlikely; and such a theory is not favored by the date (20 June) of Nelson's Santiago specimen.

Thus, available data point to a mainland coast population of *T. graysoni*, apparently not crossing freely (if at all) with the sympatric *T. rufo-palliatus*. The logical conclusion is that *Turdus graysoni* is a good species. However, additional specimens and biological data should be sought; stud-

ies of breeding pairs would be most valuable, as well as nests, eggs, juveniles, vocalizations, etc.

Once we open our eyes to the problem and abandon our preconceived idea that mainland Grayson's Robins must, perforce, be strays from the islands, it becomes unimportant whether or not they coincide exactly with island birds in color and measurements. Slight divergences between distant, well-isolated populations are only to be expected, unless one or the other has populated its present habitat within the past few centuries. (See Table 1, in which differences in technique of different workers may also be noted.)

I propose, therefore, to recognize 3 species of robins in the coastal lowlands of Nayarit: (1) Grayson's Robin, mostly along the immediate coast and poorly known, occurs inland at least to Sauta and Santiago Ixcuintla, in open country below 500 m elevation; (2) Rufous-backed Robin, widespread but apparently most numerous in woods back from the coast, the most common robin in the lowlands; and (3) White-throated Robin, abundant in the mountains and fairly common (at least formerly) in the tall forests from Compostela west and south in the lowlands, to sea-level, possibly only an irregular visitor (in small numbers?) to the woods near San Blas; recognized by the sharp line of demarcation of the clear white, unmarked lower edge of the throat against the olive-brown to grayish chest.

SUMMARY

Supposed subspecies should not be overlooked; some will later prove to be good species, when properly studied. This appears to be true of *Turdus "rufo-palliatus" graysoni*, which widely overlaps the range of *T. rufo-palliatus* in coastal Nayarit without known hybridization. Apparently 3 species are present, at least seasonally, along the coast. Field studies are badly needed.

ACKNOWLEDGMENTS

During this study I examined, or received information from the curators of the collections of the American Museum of Natural History, British Museum (Natural History) (BM), California Academy of Sciences (CAS), Carnegie Museum of Natural History (CM), Cornell University, Delaware Museum of Natural History (DEL), Institute de Biología de la Universidad Nacional Autónoma de México (MEXU), Louisiana State University Museum of Zoology (LSU), Moore Laboratory of Zoology at Occidental College (RTM), Museum of Vertebrate Zoology of the University of California (MVZ), United States National Museum of Natural History (US), University of Arizona (ARIZ) and University of New Mexico Museum of Southwestern Biology (UNM). Dr. Amadeo M. Rea and Lewis D. Yaeger provided field notes and important help in the field. Collecting permits were issued by the Departamento de Conservación de la Fauna Silvestre, México, D. F. Mary C. McKitrick kindly measured the northernmost *T. graysoni*. I am grateful to all of these, and especially to Anne Pulich for painting the frontispiece. Last but not least, I thank Elsie Marshall and Gwynne S. Leonard

for help in typing early drafts of the manuscript. Helpful comments on the manuscript were received from J. W. Aldrich, J. C. Barlow and F. G. Stiles.

LITERATURE CITED

Blake, E. R. 1953. Birds of Mexico. A guide for field identification. Univ. Chicago Press, Chicago, Illinois.

Edwards, E. P. 1972. A field guide to the birds of Mexico. Sweet Briar, Virginia.

Farner, D. S. and J. R. King. (eds.) 1971. Avian biology, Vol. I. Academic Press, New York, New York.

Grant, P. R. 1965. A systematic study of the terrestrial birds of the Tres Marías Islands, Mexico. Postilla 90:1–106.

Hellmayr, C. E. 1934. Catalogue of birds of the Americas, Pt. VII. Field Mus. Nat. Hist., Zool. Ser. XIII.

Knox, A. G. 1976. The taxonomic status of the Scottish Crossbill *Loxia* sp. Bull. Br. Ornithol. Club 96:15–19.

Marshall, J. T., Jr. 1967. Parallel variation in North and Middle American screech-owls. Monogr. West. Found. Vert. Zool. No. 1:1–72.

Miller, A. H., H. Friedmann, L. Griscom and R. T. Moore. 1957. Distributional checklist of the birds of Mexico, Pt. II. Pac. Coast Avif. 33.

Nelson, E. W. 1899. Birds of the Tres Marias Islands. N. Am. Fauna 14:7–62.

Paxton, R. O. 1979. N.Y. Rev. Books, 20 Dec., p. 14.

Phillips, A. R. 1959. The nature of avian species. J. Ariz. Acad. Sci. 1:22–30.

———. 1969. An ornithological comedy of errors: *Catharus occidentalis* and *C. frantzii*. Auk 86:605–623.

Raitt, R. J. and J. W. Hardy. 1970. Relationships between two partly sympatric species of thrushes (*Catharus*) in Mexico. Auk 87:20–57.

Ridgway, R. 1907. The birds of North and Middle America, Pt. IV. U.S. Natl. Mus. Bull. 50.

Rowley, J. S. and R. T. Orr. 1964. The status of Frantzius' Nightingale Thrush. Auk 81:308–314.

Traylor, M. A. 1979. Two sibling species of *Tyrannus* (Tyrannidae). Auk 96:221–233.

APARTADO POSTAL 370, SAN NICOLÁS DE LOS GARZA, NUEVO LEÓN, MÉXICO.
ACCEPTED 14 JAN. 1981.

COLOR PLATE

Publication of the frontispiece of the Mainland Rufous-backed Robin (*Turdus rufo-palliatus*) and Grayson's Robin (*T. graysoni*) painted by Anne Pulich has been made possible by an endowment established by George Miksch Sutton.

Wilson Bull., 93(3), 1981, pp. 310–324

HYPERPHAGIA AND SOCIAL BEHAVIOR OF CANADA GEESE PRIOR TO SPRING MIGRATION

M. Robert McLandress and Dennis G. Raveling

Several papers have emphasized the evolutionary and functional significance of spring accumulated body reserves for reproduction by geese (Barry 1962; Hanson 1962; Ryder 1970; Ankney 1977; Raveling and Lumsden 1977; Ankney and MacInnes 1978; Raveling 1978a, 1979a, b; McLandress and Raveling 1981). Numerous studies have contributed information on behavior of Canada Geese (*Branta canadensis*) (see Johnsgard 1975 and Bellrose 1976 for reviews). However, no study of wild geese has described or quantified the hyperphagia presumably associated with their increase in body weight in spring. The objective of our study was to document behavior of Giant Canada Geese (*B. c. maxima*) prior to their arrival on their nesting grounds. Emphasis was placed on behavior related to accumulation and use of energy reserves to enhance our knowledge of the evolution and proximate control of avian reproductive and social organization systems.

METHODS

We studied Giant Canada Geese wintering at Silver Lake, in the city of Rochester, Minnesota (43°55′N, 92°30′W). These birds nest between Lake Winnipeg and Lake Manitoba-Winnipegosis, in Canada, 885 km northwest of Rochester (see Hanson 1965, Gulden and Johnson 1968, Raveling 1978b). Refuges at both wintering and nesting areas of these birds and the urban environment of Rochester provided a unique situation for close observation of wild geese which were habituated to human activity. Data were collected within a 30 km radius of Rochester from 3 February–6 April 1974. The last major migration occurred on the latter date. Measurements of temperature, wind and snow cover were obtained from the U.S. Dept. of Commerce, Weather Bureau, Rochester, Minnesota.

On a daily basis, time that geese spent in feeding areas and on lake roosting areas was determined for the flock as a whole. Major flights of geese to and from these areas were visible from almost anywhere in the study area and indicated transition between feeding and roosting periods. Daily feeding regimes, defined as the duration of time spent away from lake roosting areas by at least half of the population, were categorized as follows: (A) more than half the flock did not leave lake roosting areas or left for less than 1.5 h; (B) geese were in feeding areas from 1.5–4.5 h without returning to water roost areas; (C) geese remained away from lake roosting areas from 4.5–7.5 h (usually, there were distinct morning and evening feeding periods, but one long period was normal on overcast days); (D) geese were in feeding areas from 7.5–10.5 h during the day, typically in one continuous period; and (E) geese spent more than 10.5 h in feeding areas because at least half the flock did not return to lake roosting areas for at least part of the night.

Over 200 individually identifiable neck-banded adult geese were available for observation (see Raveling 1978b). Numbers of geese in feeding areas were estimated when possible and all marked birds observed were recorded. The proportion of time spent in these fields actually

devoted to feeding by marked individuals (and their mates, when present) was recorded for sample periods of approximately 10 min (timed by stopwatch).

Family status of geese was determined from behavioral associations (see Raveling 1969), especially the triumph ceremony. This display involves extensive head and neck movements with associated vocalizations and is usually exhibited only by mated pairs of adults and among members of a family (see Fischer 1965, Raveling 1970). The occurrence of triumph ceremonies and aggressive interactions involving physical contact between individuals were recorded for timed periods averaging 30 min.

The number of sexual displays was recorded when a majority of the goose population was at Silver Lake. Approximately 1000 birds were observed when sexual displays were being recorded so as to have reasonably comparable samples from which to compare rates of sexual behaviors. Sexual behavior noted included copulation and the pre-copulatory neck-dipping display (Klopman 1962). Sperm transfer could not be determined but copulation was considered unsuccessful only when the post-copulatory display (Klopman 1962) was not exhibited by either sex following coition. Size and behavior of unmarked geese was used to identify sex of the individual initiating neck-dipping and terminating incomplete sexual displays when possible.

Proportions of timed sample periods spent feeding by individuals and frequencies of triumph ceremonies and aggressive interactions, measured as the number of displays or contacts per unit time per bird, were ranked and analysed with Mann-Whitney *U*-tests (Sokal and Rohlf 1973:218). Changes in intensity of triumph ceremonies and aggressive interactions, which were categorized according to vigor and duration of displays (see description in Results), were compared with Chi-square tests (Sokal and Rohlf 1973:300). Significance of the regression of changes in frequency of sexual behavior over time was also tested (Sokal and Rohlf 1973:248).

RESULTS

Changes in food habits and body composition determined from geese collected during this study are reported elsewhere (McLandress and Raveling 1981). In summary, the results were: (1) body weight of adult female and male geese increased 36% and 26%, respectively, above average winter (February) weights; (2) adult geese without mates weighed less before the weight gain period and gained less weight than paired geese; (3) geese shifted from a winter diet of corn (*Zea mays*) to a diversity of food items in spring dominated by bluegrass (*Poa pratensis*); and (4) bluegrass was rich in protein (>26%), which is a requirement that may limit clutch-size in Canada Geese (Raveling 1979a).

Feeding behavior.—Ambient temperatures ranged from −28 to 16°C. Under the coldest conditions geese remained at Silver Lake with bills tucked under their scapular feathers. As temperature increased, geese spent more time in feeding areas (Table 1: $r = 0.87$, $P < 0.001$). This resulted in geese feeding 7.5 h or longer (category D or E), for 25 of 34 days (74%) for which feeding regime data were obtained from 1 March to the 6 April mass migration. Only 5 extended feeding regimes (22%) were recorded for 23 days of data between 3 and 28 February. Geese fed during the night (category E) only when temperatures remained above or near 0°C between

Table 1

Daily Feeding Pattern of Giant Canada Geese Under Different Temperatures Prior to Spring Migration (3 February–6 April 1974)[a]

Feeding regime[b]	Max. / Min.	Daily temperature ranges (°C)					
		<−10° <−10°	−10°–−5° <−10°	>−5° <−10°	>−5° −10°–−5°	>−5° −5°–0°	>0° >0°
A (0–1.5 h)		2[c]	1				
B (1.5–4.5 h)			7	2			
C (4.5–7.5 h)			2	7	5	1	
D (7.5–10.5 h)				1	7	15	3
E (>10.5 h)						1	3
Total days		2	10	10	12	17	6

[a] No data for 6 days within this period.
[b] See text.
[c] Actual daylight maximum temperatures for these days were −16°C and −13°C.

2 and 6 March. These warm nights, although partially overcast, coincided with a full moon. Patterns of decreased feeding (category B or C) returned 17–24 March when minimum temperatures were less than −5°C and maximums were seldom above 0°C.

Changes in feeding location corresponded with decreasing snow depth in February (Table 2). Geese fed rarely in grass fields and frequently in creeks and ponds when recorded snow depth was greater than 20 cm. Geese were more dispersed when at creeks and ponds than when in cornfields. Thawing occurred first around the bases of trees and where clumps of vegetation extended through the snow. These snow-free patches exposed grass when recorded snow depth fell below 20 cm. Geese fed at these patches as soon as they appeared. Snow was 18 cm deep on 1 March and all but gone by 6 March. Snow fell on 6 days after 11 March but accumulation did not exceed 8 cm for the remainder of the study.

Corn remained an important food item throughout the study. Waste corn, frozen in top soil, became available to geese as the soil thawed (9–16 March). More geese in feeding areas were observed in cornfields in this week than during any other time period when snow depth was less than 20 cm. Proportions of feeding geese that used pastures increased after 25 March and peaked just before the 6 April migration. Generally, geese fed in cornfields and pastures bordering creeks and rivers flowing into Silver Lake.

The average size of the Giant Canada Goose population during our study was 12,000–15,000 birds. Thirty-one flocks of geese feeding in cornfields of approximately 65 ha (160 acres) averaged 1996 ± 311 birds during February. Flock size in cornfields in early March (869 ± 111 birds, N = 123

TABLE 2

FEEDING LOCATIONS OF GIANT CANADA GEESE PRIOR TO SPRING MIGRATION, 1974

Date	Total geese observed[a]	% of geese in:		
		Corn	Grass	Creeks and ponds
Snow depth >20 cm:				
3–28 February	30,290	86	1	13
Snow depth <20 cm:				
3–28 February	36,197	63	36	1
1–8 March	44,870	62	31	6
9–16 March	40,580	86	11	3
17–24 March	46,620	71	24	5
25 March–1 April	72,063	47	51	2
2–6 April	16,842	38	62	0

[a] Summation of all geese in feeding flocks estimated to size; most flocks were repeatedly observed over the time period—see text for average flock size.

flocks) was significantly smaller ($t = 4.16$, $P < 0.001$) and it diminished still further ($t = 4.52$, $P < 0.001$) to 339 ± 35 geese (N = 122 flocks) in the 2 weeks prior to the 6 April migration. Decreasing flock size was related to an increase of distance between individuals. No significant change was detected in flock size of grass feeding geese among comparable time periods. Geese feeding in 65 ha (160 acres) pastures averaged 360 ± 42 geese (N = 183 flocks).

Proportions of marked geese of known social status feeding in grass changed markedly ($\chi^2 = 8.89$, df = 2, $P < 0.002$) during spring (Table 3). The percentage of marked birds that were paired declined slightly as spring progressed, although the actual number of paired geese showed little change. In contrast, the number of marked geese never observed with a mate doubled between each observation period from early to late

TABLE 3

PROPORTIONS OF INDIVIDUALLY MARKED ADULT GIANT CANADA GEESE OF DIFFERENT SOCIAL STATUS OBSERVED IN GRASS FIELDS DURING SPRING 1974

Date	N	Status		
		Paired	Unpaired	Undetermined
18 February–9 March	56	44 (79%)	5 (9%)	7 (13%)
9–24 March	69	53 (77%)	10 (15%)	6 (9%)
24 March–6 April	79	49 (62%)	22 (28%)	8 (10%)

TABLE 4

PROPORTION OF TIME ACTUALLY DEVOTED TO FEEDING BY GIANT CANADA GEESE OF DIFFERENT SEX AND SOCIAL STATUS DURING SPRING (3 FEBRUARY–6 APRIL 1974)

Sex and social status of geese	Feeding site			
	N[a]	Cornfield	N[a]	Grass field
Males				
In pairs	31	38%[b] 26–53[c]	20	51% 45–77
Others	55	38% 32–52	30	64% 37–81
Females				
In pairs	32	52% 39–62	22	65% 54–79
Others	51	24% 17–33	37	52% 36–79

[a] Number of approximate 10 min sample periods in which a marked individual's proportion of time spent feeding was recorded.
[b] Median.
[c] Confidence limits (cf. Snedecor and Cochran 1967:124).

spring. Accurate determinations of social status of geese in cornfields were difficult in February and early March due to large flock sizes.

While in grass fields, paired geese spent higher proportions of their time actually feeding than when they were in cornfields (Table 4: $t_s = 1.66$ males and 1.83 females, $P < 0.05$). Similarly, "other" females (referring to individuals without identifiable mates in the vicinity) spent a higher proportion of time feeding while in pasture than in cornfields ($t_s = 3.60$, $P < 0.001$). "Other" males showed a tendency toward the same feeding pattern ($t_s = 1.59$, $P < 0.1$). Paired females tended to feed for a greater proportion of time than paired males when in either cornfields ($t_s = 1.50$, $P < 0.1$) or grass fields ($t_s = 1.49$, $P < 0.1$). Also, when both members of a pair were observed simultaneously, females spent more time feeding than males on 73% of observations (N = 63). Proportions of time spent feeding by "other" and paired males were similar but "other" females spent less time feeding when in cornfields than either paired females ($t_s = 3.60$, $P < 0.001$) or "other" males ($t_s = 2.85$, $P < 0.005$).

Social behavior.—No significant differences were detected among frequencies of triumph ceremonies determined from observations at Silver Lake, either among periods of time during the day (i.e., morning—07:00–10:00, mid-day—10:00–15:00 and evening—15:00–19:00) or between February and March. A significantly higher frequency ($t_s = 3.45$, $P < 0.001$)

TABLE 5

FREQUENCY AND INTENSITY DIFFERENCES OF TRIUMPH CEREMONY DISPLAYS AND AGGRESSIVE INTERACTIONS OF GIANT CANADA GEESE AT AND AWAY FROM SILVER LAKE DURING SPRING 1974

	Silver Lake		Other areas	
	3–28 Feb.	1 Mar.–6 Apr.	3–28 Feb.	1 Mar.–6 Apr.
	Triumph ceremonies (T.C.)			
Frequency[a]				
Median (N)[b]	2.6 (26)	5.4 (6)	12.0 (5)	20.0 (2)
95% C.L.	1.9–4.8	1.3–7.5	3.3–38.0	13.3–26.7
Intensity				
T.C.'s categorized	199.0	60	37	24
Reduced (%)	19.1	42	3[b]	17[b]
Normal (%)	63.3	42	32	46
Exaggerated (%)	17.6	17	65	38
	Aggressive interactions (A.I.)			
Frequency[a,d]				
Median (N)	0.5 (6)	5.3 (3)	8.2 (4)	24.4 (2)
95% C.L.	0.0–2.7	1.3–6.7	8.0–12.0	10.7–38.1
Intensity				
A.I.'s categorized	114.0	35	31	28
Pecking (%)	36.8	69	29	36
Chasing (%)	49.1	23	61	54
Fighting (%)	14.0	9	10[b]	11[b]

[a] Displays/1000 birds/min.
[b] N = number of observation periods (ca. 30 min each).
[c] Combined with closest category for χ^2 test due to infrequent occurrence.
[d] Mid-day (10:00–15:00) observations only.

of displays was recorded for observations in areas other than Silver Lake compared to Silver Lake in March (Table 5).

Triumph ceremony intensity was classified "normal" when the components (see Raveling 1970), rolling (neck extended upward and forward) and cackling (neck extended downward and forward), were displayed with about equal frequency. Intensity was considered "reduced" when: wing-flicking (shown to some extent during "normal" displays) was not exhibited by either adult; cackling exceeded rolling; head and neck waving during the rolling component were more restricted; and vocalizations were less raucous and prolonged than in "normal" triumph displays. "Exaggerated" displays involved vigorous rolling by males and extended raucous vocalizations. The criterion for classification in this category was that contact was made between adults. Typically, adult males used their bills to grasp

the female's neck near the back of her head or base of the black neck stocking. Occasionally, females grasped the breast feathers of males.

There was a significant change in proportions of triumph ceremony displays of different intensity exhibited at Silver Lake (Table 5: $\chi^2 = 13.38$, df = 2, $P < 0.005$) and at areas other than Silver Lake ($\chi^2 = 4.39$, df = 1, $P < 0.05$) between February and March. "Reduced" intensity displays increased at all areas. Little change occurred in the proportion of "exaggerated" intensity displays at Silver Lake but these were greatly reduced at other areas. The percentage of "normal" displays was less in March than in February at Silver Lake.

Proportions of triumph ceremonies of different intensity at areas other than Silver Lake differed significantly from displays at Silver Lake in February ($\chi^2 = 38.06$, df = 2, $P < 0.001$) and in March ($\chi^2 = 6.46$, df = 2, $P < 0.05$). At areas other than Silver Lake, highly vigorous displays were much more common (or "reduced" intensity triumph ceremonies were much less common) than at Silver Lake.

Triumph ceremonies were most commonly associated with aggressive conflicts among geese (76% of 191 displays for which circumstances were recorded). Pairs often displayed prior to conflict and immediately following retreat of an opponent. The intensity of display increased with the duration of aggressive interaction and the degree of physical conflict. Most triumph ceremonies associated with aggressive conflicts (N = 145) were classified as either "normal" (47%) or "exaggerated" (33%) in intensity. Aggressive interactions were involved in 48 (94%) of the 51 most intense triumph ceremonies.

If mated pairs were spatially separated for any reason, triumph ceremony occurred when they were reunited. In March, triumph ceremony was occasionally (9 times) observed when 1 member of a pair involved had just awakened (separation in a temporal sense). Triumph ceremonies following either type of separation comprised 24% of the 191 displays. Proportionately fewer high intensity displays and more low intensity displays were noted for triumph ceremonies following separation of mates ("exaggerated" = 7%, "normal" = 50%, "reduced" = 43%, N = 46) than for triumph ceremonies related to aggression ($\chi^2 = 16.82$, df = 2, $P < 0.001$). The proportion of "reduced" intensity displays was highest for triumph ceremonies related to reunion of mates after awakening (7 of 9, 78%).

Only frequencies of aggressive interactions obtained from observations at mid-day (10:00–15:00) are presented (Table 5) because significant differences were found among different time periods of the day and too few observations were taken during other time periods for further comparisons. A difference in frequency of interactions was detected for these mid-

day observations between February and March at Silver Lake ($U_s = 17$, $P < 0.025$). In addition, geese at locations away from Silver Lake were involved in higher frequencies of aggressive encounters than geese at Silver Lake ($U_s = 54$, $P < 0.001$).

A total of 208 aggressive interactions between geese were classified according to degree of physical exertion (Table 5). "Pecking" involved 1 goose striking another with its bill, followed by a short retreat or immediate submission by the loser. "Chasing" was characterized by the victorious goose chasing the loser with no fighting involved. "Fighting" referred to encounters in which 2 geese grasped each other at the base of the neck with their bills and hit each other with their wings. Proportions of aggressive encounters of different physical involvement observed at Silver Lake in March changed significantly from proportions recorded for geese in February aggressive encounters ($\chi^2 = 11.01$, df = 2, $P < 0.005$). The proportion of aggressive encounters which involved "pecking" doubled from February–March and because the frequency of conflicts was greater, the absolute amount of "chasing" and "fighting" may have increased as well. These differences between months were not evident at areas other than Silver Lake. There was a significant difference in the proportion of interactions of different exertion between geese at and away from Silver Lake in March ($\chi^2 = 6.76$, df = 1, $P < 0.01$), but not in February.

Sexual behavior.—Copulation attempts by geese were observed 69 times during spring although 6 (9%) were considered incomplete due to lack of the post-copulatory display. In addition, the pre-copulatory display, neck-dipping, was not followed by coition on 67 occasions. The frequency of all sexual behaviors (which included successful copulation, neck-dipping not followed by coition and unsuccessful copulation) increased exponentially from 3 February–6 April (Fig. 1: $Y = 0.05e^{0.60X}$, $t_s = 5.72$, $P < 0.001$). Although the highest rate of sexual displays was recorded in the first week of April, only 8% (1 of 13) of sexual interactions resulted in successful coition compared to 53.6% (60 of 112) for March sexual displays ($\chi^2 = 9.81$, df = 1, $P < 0.005$). The frequency of successful copulations was highest in the last week of March.

Males initiated neck-dipping on 19 of 27 (70%) occasions when sexes of both members of the pair were identified—a significantly higher proportion than an expected equal contribution by each sex ($\chi^2 = 4.48$, df = 1, $P < 0.05$). The copulatory behavior sequence was terminated by the female before coition on 14 of 20 (70%) observations when sex of the birds could be determined, which tended to be a higher rate than would be expected from equal contribution by either sex ($\chi^2 = 3.20$, df = 1, $P < 0.10$). Similar findings were reported by Klopman (1962).

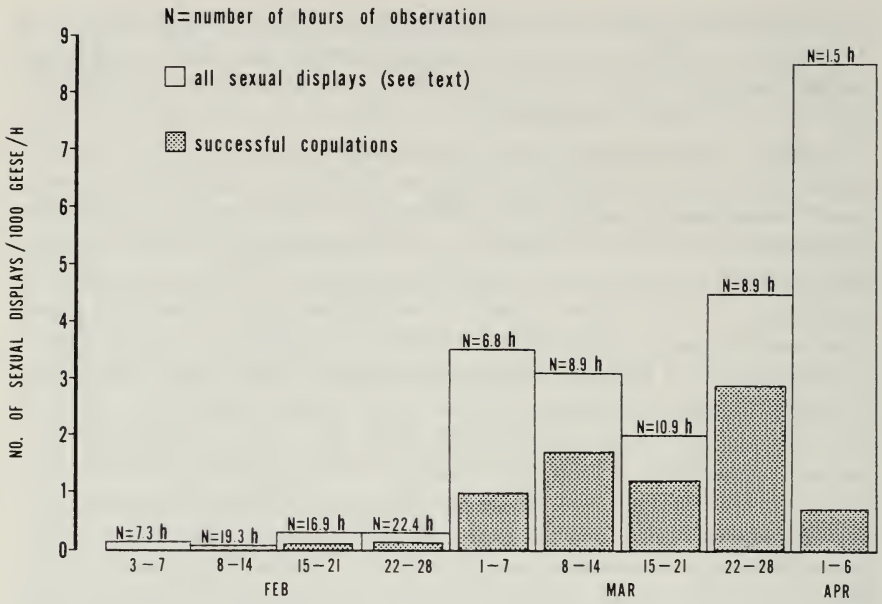


FIG. 1. Frequency of displays of the copulatory sequence of Giant Canada Geese during spring 1974.

DISCUSSION

Environmental factors affecting food consumption.—Daily ambient temperature range appeared to influence the amount of time spent in feeding areas by Giant Canada Geese during spring. Raveling et al. (1972) reported that cold had little influence on the length of the feeding period of Todd's Canada Geese (*B. c. interior*) in southern Illinois and concluded that cloudy conditions caused them to spend more time in feeding areas in winter. In this study, temperature seemed to be the most important influence on daily duration of feeding by geese. Cloud cover was, however, related to patterns of feeding. Geese usually had distinct morning and evening feeding periods on clear days, whereas, on cloudy days of similar temperature ranges they typically had single feeding periods of prolonged duration, but total time per day spent in feeding areas was unchanged.

Higher temperatures melted snow and thawed soil enabling geese to use previously inaccessible food resources. These conditions corresponded with geese spending all day and some nights in feeding areas. In contrast to the results of this study, *B. c. interior* held in captivity and supplied food ad libitum, increased energy intake with decreasing ambient temperature regardless of photoperiod (Williams 1965). However, Raveling et al. (1972) reported that temperatures at or below −9°C (15°F) caused wild

B. c. interior to cease activity. Similarly, in this study, on 2 days when temperature remained below −13°C (9°F), geese stayed at Silver Lake. LeFebvre and Raveling (1967) predicted that immature female Giant Canada Geese could not sustain the energetic demand caused by prolonged heat loss at temperatures less than −15°C (5°F). Raveling et al. (1972) suggested that inactivity which reduces energy loss is the most adaptive response of geese to extreme cold. Thus, the behavioral response of Canada Geese to changing energetic demands is flexible and can be altered by increased food availability. After appropriate photo-stimulation (see reviews by Lofts and Murton 1968, 1973; Farner and Lewis 1971; Lofts 1975), the expression of hyperphagia by geese may be regulated by temperature and food availability in spring. Such control would maximize positive energy balance during the fattening period.

The insulating effect and translucent quality of snow may provide sufficient warmth and light for survival and early germination of grasses in years of ample snow cover (see Tieszen 1972). During the spring of 1974, geese were able to obtain protein-rich green grass (McLandress and Raveling 1981) from beneath melting snow 11 days prior to the major thaw in early March. Winters with little precipitation or frequent thawing of snow cover could result in decreased survival of subnivean grass and delay in the emergence of new grasses. Conversely, mild spring weather might allow geese earlier access to grasses.

Social factors and food intake.—Appropriate behavior between members of pairs is necessary for follicle maturation in many birds (see review by Lofts and Murton 1973). Results of our study indicate that pair relations may also be important to spring fat accumulation. All geese spent a greater percentage of time devoted to feeding when in grass fields than in cornfields. Paired geese preceded non-paired birds to grass fields in spring and paired females spent more time actually feeding when in cornfields than unpaired females. Finally, unpaired geese initially weighed less and gained less weight in the period of fat accumulation (McLandress and Raveling 1981).

Decreases in density of flocks of geese feeding in cornfields could have been due to diminishing amounts of waste corn as spring progressed. However, density of flocks in pastures remained unchanged and essentially equaled the final density of geese recorded for cornfields in spring. A higher percentage of geese feeding in pastures coincided with the decrease in density of flocks of geese feeding in cornfields. Flocks of geese feeding in pastures contained higher proportions of unpaired geese in the 2 weeks prior to spring migration than earlier in spring. Possibly, this reflects later initiation of hyperphagia in potentially non-reproductive geese.

The preponderance of rolling and cackling components of triumph ceremonies displayed in different releasing situations in this study were not as clearly separable as Fischer (1965) reported for Greylag Geese (*Anser anser*). Rather, these components appeared to form a continuum from exclusively cackling in the mildest triumph ceremonies, to predominantly rolling in displays of the highest intensity. Rolling is almost exclusively a male behavior and has been accepted as a predominantly aggressive display (Lorenz 1959, Fischer 1965, Raveling 1970, Radesater 1974). Radesater (1974) suggested that the frequency of rolling may depend on testosterone levels as frequency increased during seasons when agonistic encounters were common in captive geese. The decrease in proportion of "exaggerated" (rolling predominated) triumph ceremonies by Giant Canada Geese as well as the lower proportion of "chasing" and "fighting" noted in aggressive interactions as spring progressed, would appear to contradict a correlation with higher testosterone levels indicated by increasing testis size (McLandress and Raveling, unpubl.). However, geese became progressively more dispersed in feeding areas through spring, thus reducing intensity and/or frequency of agonistic stimuli. Less conspicuous chasing and threatening behavior than during winter has also been reported for Canada Geese upon their arrival at the breeding grounds in spring (Raveling and Lumsden 1977).

As spring progressed, the frequency of triumph ceremonies did not change significantly despite a decrease in the proportion of aggressive related displays. The lower proportions of "normal" and "exaggerated" displays were balanced by an increasing number of "reduced" intensity triumph ceremonies. "Reduced" intensity triumph ceremonies (predominated by cackling) observed in this study, as in other studies (Lorenz 1959, Fischer 1965, Raveling 1970, Radesater 1974), often occurred in the absence of agonistic stimuli. Hanson (1953) and Raveling (1970) concluded that families and mates remaining together have an adaptive advantage in the social hierarchy of Canada Geese in winter. The dominance order provides benefits in terms of food and space acquisition, and reduction of aggressive encounters. The higher number of "reduced" intensity triumph ceremonies may be a reflection of increased stimulation of geese to be with mates in spring. This would be adaptively advantageous to: (1) enhance the status of paired geese in the dominance hierarchy during the period of hyperphagia, nest-site selection and territorial defense; (2) insure that pairs arrive together on the breeding grounds; and (3) stimulate pair formation in unmated geese.

Termination of spring hyperphagia.—Raveling (1978a) concluded that factors that stimulate the gonadotropin release responsible for follicle maturation in female Canada Geese occur at the same time as, or just before,

final migration to nesting grounds. The yolk of eggs of Canada Geese takes 12–13 days to develop (Raveling 1978a). Geese in this study migrated 2–6 April, arrived on nesting grounds on 8 and 9 April and began egg-laying 19 and 20 April. However, nest initiation was probably delayed by a lack of meltwater at nest-sites (see also Cooch 1958, 1961; Barry 1962, 1967; MacInnes 1962; Ryder 1967; Mickelson 1975). Minor follicular development had occurred in female geese collected during March, but rapid yolk deposition was evident only in geese collected 4–6 April. Based on average size of the largest follicles of 4 females collected 4–6 April (23 mm; McLandress and Raveling, unpubl.), it is likely that rapid ovarian follicular development began during the last week of March.

Digestive organs which were enlarged in geese collected 14–16 March had decreased in size in birds collected 4–6 April (McLandress and Raveling, unpubl.) indicating that hyperphagia had already ended. The exponential increase in sexual displays (Fig. 1) during spring corresponded with enlargement of testes and ovarian follicle size of collected geese (McLandress and Raveling, unpubl.). Despite the highest frequency of displays of the sexual sequence occurring in the first week of April, copulatory success indicated that the most important week for coition was 21–28 March. Coincidentally, 9 of 15 (60%) post-copulatory displays, for which information was recorded during the week of 21–28 March, included the female. This frequency was significantly greater ($\chi^2 = 6.84$, df = 1, $P < 0.01$) than 4 female postcopulatory displays of 22 (18%) copulations observed throughout spring by Klopman (1962). Thus, rapid ovarian follicle growth began before migration, coincided with the decrease in size of digestive organs enlarged during hyperphagia, and was correlated with and perhaps, as suggested by Raveling (1978a), stimulated by copulatory behavior.

Giant Canada Geese of this study population have consistently arrived on their nesting grounds in Manitoba between 5 and 9 April, 1968–1975 (Raveling, unpubl.). Day length, the most consistent indicator of season (Follett 1973), is likely the primer for migration and associated physiological changes. Secondary factors may modify timing of migration, final development of ovarian follicles and termination of hyperphagia, once photoperiod is permissive.

Hyperphagia and the resulting weight gain of geese began 1 March when warming temperatures and melting snow allowed geese to have prolonged access to new grass. Pre-reproductive body weight gain was attained by the end of March. Young grass eaten by geese contained high levels (>26%) of protein (McLandress and Raveling 1981). Young grass remains highly digestible for approximately 1 month during spring, at which time digestibility abruptly decreases (McDonald et al. 1973). Thus, duration of

the fattening period of Canada Geese and their use of fertile lowlands along creeks coincided with availability of maximum quality of grass. Cold weather which was related to reduced feeding efforts occurred 17–24 March. Perhaps the required increase of weight could occur more rapidly in years of even more clement weather.

SUMMARY

Behavioral changes of Giant Canada Geese associated with accumulation of body weight prior to spring migration were studied in southeastern Minnesota. Daily duration of time spent in feeding areas by geese increased with increasing temperature. The percentage of geese feeding in grass fields increased, but cornfields remained important feeding sites throughout spring. Adult geese spent more time actually feeding when in pastures than when in cornfields. Paired females devoted more time to feeding than males in either cornfields or pastures and more time than females without mates in cornfields. Increased dispersal of geese in spring coincided with proportionately fewer vigorous triumph ceremonies and a lower percentage of aggressive encounters which involved actual fighting. However, the frequency of all triumph ceremonies and aggressive encounters may have increased. Sexual behavior increased exponentially through spring, but the highest frequency of successful copulations coincided with the onset of rapid yolk formation and with the termination of hyperphagia 1 week prior to migration. Hyperphagia and the associated accumulation of body reserves by Giant Canada Geese occurred in a period of less than 1 month prior to departure for the breeding grounds which coincided with availability of the highest level of protein in new growth grass.

ACKNOWLEDGMENTS

This research was supported by National Science Foundation grant GB-38788. We are grateful for permission from the P. Curry and A. Vincent families to study at East Meadows Ranch, Manitoba, and from the Rochester Parks Board and the Minnesota Department of Natural Resources (MDNR) to study at Silver Lake, Rochester. N. Gulden, R. Holmes and R. Jessen (MDNR) supplied equipment and handled many administrative matters. J. Gilbertson (MDNR) and G. Yaeger of the Rochester Post Bulletin were invaluable in dealing with public relations. Many thanks are due to A. Stegen (MDNR). L. Salata and M. Wege of the University of California, Davis (UCD) for their assistance in the field. Additional help was provided by R. Christman of Macalester College, L. King, Manager of East Meadows Ranch, and K. Brace of the Canadian Wildlife Service. R. Schwab and W. Hamilton (UCD) provided valuable critiques of early drafts. We are especially grateful to Ilse McLandress who helped with fieldwork and typed earlier drafts of the manuscript.

LITERATURE CITED

Ankney, C. D. 1977. The use of nutrient reserves by breeding male Lesser Snow Geese *Chen caerulescens caerulescens*. Can. J. Zool. 55:1984–1987.

——— and C. D. MacInnes. 1978. Nutrient reserves and reproductive performance of female Lesser Snow Geese. Auk 96:459–471.

Barry, T. W. 1962. Effect of late seasons on Atlantic Brant reproduction. J. Wildl. Manage. 26:19–26.

———. 1967. The geese of Anderson River Delta, Northwest Territories. Ph.D. thesis, Univ. Alberta, Edmonton, Alberta.

Bellrose, F. C. 1976. Ducks, geese and swans of North America. Stackpole Books, Harrisburg, Pennsylvania, and Wildl. Manage. Inst., Washington, D.C.

Cooch, F. G. 1958. The breeding biology and management of the Blue Goose (*Chen caerulescens*). Ph.D. thesis, Cornell Univ., Ithaca, New York.

———. 1961. Ecological aspects of the Blue-Snow Goose complex. Auk 78:72–89.

Farner, D. S. and R. A. Lewis. 1971. Photoperiodism and reproductive cycles in birds. Pp. 325–370 *in* Photophysiology, Vol. 5 (A. C. Giese, ed.). Academic Press, New York, New York.

Fischer, H. 1965. Das Triumphgeschrei der graugans (*Anser anser*). Z. Tierpsychol. 22:247–304.

Follett, B. K. 1973. The neuroendocrine regulation of gonadotropin secretion in avian reproduction. Pp. 209–243 *in* Breeding biology of birds (D. S. Farner, ed.). Natl. Acad. of Sci., Washington, D.C.

Gulden, N. A. and L. L. Johnson. 1968. History, behavior and management of a flock of Giant Canada Geese in southeastern Minnesota. Pp. 59–71 *in* Canada Goose management (R. L. Hine and C. Schoenfeld, eds.). Dembar Educ. Res. Serv., Madison, Wisconsin.

Hanson, H. C. 1953. Inter-family dominance in Canada Geese. Auk 70:11–16.

———. 1962. The dynamics of condition factors in Canada Geese and their relation to seasonal stresses. Arctic Inst. N. Am. Tech. Pap. No. 12.

———. 1965. The Giant Canada Goose. S. Illinois Press, Carbondale, Illinois.

Johnsgard, P. A. 1975. Waterfowl of North America. Indiana Univ. Press, Bloomington, Indiana.

Klopman, R. B. 1962. Sexual behavior in the Canada Goose. Living Bird 1:123–129.

Lefebvre, E. A. and D. G. Raveling. 1967. Distribution of Canada Geese in winter as related to heat loss at varying environmental temperatures. J. Wildl. Manage. 31:538–546.

Lofts, B. 1975. Environmental control of reproduction. Pp. 176–197 *in* Avian physiology (M. Peaker, ed.). Academic Press, New York, New York.

——— and R. K. Murton. 1968. Photoperiodic and physiological adaptations regulating avian breeding cycles and their ecological significance. J. Zool. 155:327–394.

——— and ———. 1973. Reproduction in birds. Pp. 1–107 *in* Avian biology, Vol. 3 (D. S. Farner and J. R. King, eds.). Academic Press, New York, New York.

Lorenz, K. 1959. The role of aggression in group formation. Pp. 181–252 *in* Group processes: transactions of the fourth conference (B. Schaffner, ed.). Josiah Macy, Jr. Foundation, New York, New York.

MacInnes, C. D. 1962. Nesting of small Canada Geese near Eskimo Point, Northwest Territories. J. Wildl. Manage. 26:247–256.

McDonald, P., R. A. Edwards and J. F. D. Greenhalgh. 1973. Animal nutrition. Hafner Publ. Co., New York, New York.

McLandress, M. R. and D. G. Raveling. 1981. Food habits and body composition changes of Giant Canada Geese prior to spring migration. Auk 98:65–79.

Mickelson, P. G. 1975. Breeding biology of Cackling Geese and associated species on the Yukon-Kuskokwim Delta, Alaska. Wildl. Monogr. 45.

Radesater, T. 1974. Form and sequential associations between the triumph ceremony and other behaviour patterns in the Canada Goose *Branta canadensis* L. Ornis Scand. 5:87–101.

Raveling, D. G. 1969. Social classes of Canada Geese in winter. J. Wildl. Manage. 33:304–318.

———. 1970. Dominance relationships and agonistic behavior of Canada Geese in winter. Behaviour 37:291–319.

———. 1978a. The timing of egg laying by northern geese. Auk 95:294–303.
———. 1978b. Dynamics of distribution of Canada Geese in winter. N. Am. Wildl. and Natl. Res. Trans. 43:206–225.
———. 1979a. The annual cycle of body composition of Canada Geese with special reference to control of reproduction. Auk 96:234–252.
———. 1979b. The annual energy cycle of the Cackling Canada Goose. Pp. 81–93 *in* Management and biology of Pacific flyway geese: a symposium (R. L. Jarvis and J. C. Bartonek, eds.). OSU Bookstores, Inc. Corvallis, Oregon.
———, W. E. Crews and W. D. Klimstra. 1972. Activity patterns of Canada Geese during winter. Wilson Bull. 84:278–295.
——— and H. G. Lumsden. 1977. Nesting ecology of Canada Geese in the Hudson Bay lowlands of Ontario: evolution and population regulation. Ont. Min. Nat. Res. Fish and Wildl. Res. Rept. No. 98.
Ryder, J. P. 1967. The breeding biology of Ross' Goose in the Perry River region, Northwest Territories. Can. Wildl. Serv. Rept. Ser. No. 3. Ottawa, Ontario.
———. 1970. A possible factor in the evolution of clutch size in Ross' Goose. Wilson Bull. 82:5–13.
Snedecor, G. W. and W. G. Cochran. 1967. Statistical methods, 6th ed. Iowa State Univ. Press, Ames, Iowa.
Sokal, R. R. and F. Rohlf. 1973. Introduction to biostatistics. W. H. Freeman and Company, San Francisco, California.
Tieszen, L. L. 1972. The seasonal course of above ground production and chlorophyll distribution in a wet Arctic tundra at Barrow, Alaska. Arctic and Alpine Res. 4:307–324.
Williams, J. E. 1965. Energy requirements of the Canada Goose in relation to distribution. Ph.D. thesis, Univ. Illinois, Urbana, Illinois.

DEPT. WILDLIFE AND FISHERIES BIOLOGY, UNIV. CALIFORNIA, DAVIS, CALIFORNIA 95616. ACCEPTED 20 SEPT. 1980.

RESEARCH GRANTS

The Eastern Bird Banding Association and the Western Bird Banding Association are each offering a research grant of $250 in aid of research using bird banding techniques or bird banding data. Applicants should submit a resume of his or her banding or ornithological background, the project plan and a budget to the joint selection committee chairman: Robert C. Leberman, Powdermill Nature Reserve, Star Route South, Rector, Pennsylvania 15677. No formal application forms are available, and the amount requested should not exceed $250. The deadline for receipt of applications is 15 March 1982.

Wilson Bull., 93(3), 1981, pp. 325–333

A MULTIPLE SENSOR SYSTEM FOR MONITORING AVIAN NESTING BEHAVIOR

James A. Cooper and Alan D. Afton

Avian nest construction, laying and incubation time budgets often provide a temporal framework for ethological, physiological and ecological investigations. Numerous methods have been devised to measure nest attentive and inattentive periods. Early approaches, reviewed by Kendeigh (1952:5) and Skutch (1962), involved observations from a blind or simple mechanical switch devices connected to graphic recorders. Advances in electronic and photographic equipment have led to the development of many useful instruments for detecting the presence of birds at or near nests. Thermistors and thermocouples have been positioned in nests (Baldwin and Kendeigh 1927, Farner 1958, Norton 1972), in eggs (Huggins 1941, Snelling 1972, Caldwell and Cornwell 1975 and others), or in artificial eggs (Holstein 1942, Kossack 1947, Norton 1972). Photoelectric sensors were placed in or near nests by Kessler (1962) and Weeden (1966), while time lapse cameras were used by Weller and Derksen (1972) and Caldwell and Cornwell (1975). Gilmer et al. (1971), Varney and Ellis (1974) and Miller (1976) have described telemetry systems. Pulliainen (1978) recently employed closed-circuit television to record nesting behavior.

Each approach reflected the limitations imposed by the species studied, the availability and cost of electronic and photographic equipment and the inventiveness of the investigator(s). Skutch (1962) emphasized, and we believe correctly, that automatic monitors cannot substitute for observation. Yet, investigations of individual variation or nocturnally active birds cannot easily be done by observation alone. Nocturnal observations require expensive night-vision equipment, and large samples are necessary for statistical analysis of differences among individual birds. Varney and Ellis (1974) criticized thermistor and thermocouple techniques because a wire must be attached to an egg; they recommended a telemetry system in an artificial egg. However, artificial egg temperatures differ from heat levels in developing eggs (Drent 1970). Earlier methods used a single sensor, not allowing crosschecking for accuracy or simultaneous monitoring of egg temperatures, incubating bird behavior or identity.

This paper describes the construction and field application of a multiple sensor (photoelectric-thermistor-photographic) system for nesting studies. While employed primarily in waterfowl investigations to date, the apparatus has potential for studies of a wide range of species.

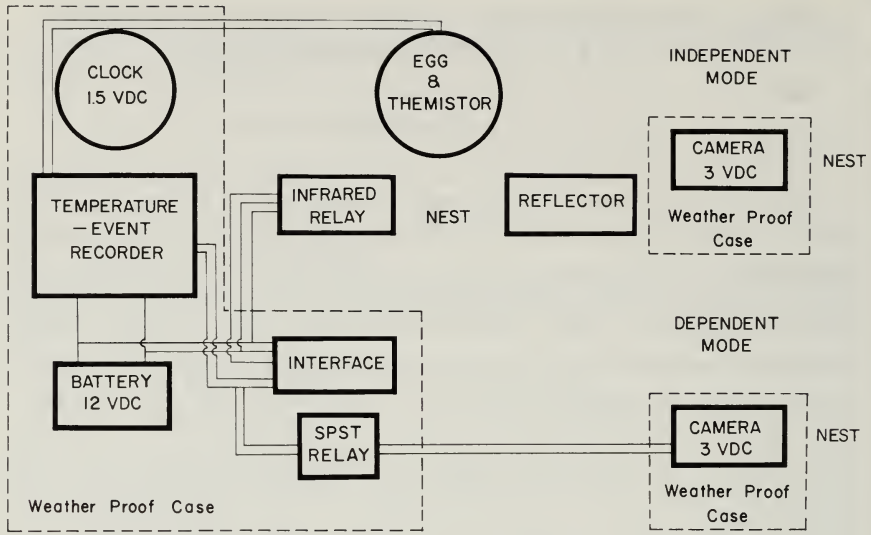


FIG. 1. Block diagram of the multiple sensor system.

METHODS AND MATERIALS

Instrument design and construction.—Basic instrument components are: an infrared photoelectric relay (Microswitch MLS-3A), a medical thermistor (Rustrak 1331), a super-8 movie camera (Minolta XL-401), a strip-chart, temperature-event recorder (Rustrak 2133), an infrared relay interface and a 1.5 VDC clock (Fig. 1). The recorder, interface and clock are housed in a weather-proof case. The infrared relay and camera are positioned near or at the nest and connected to the recorder and interface, and the thermistor probe is inserted in an egg or in the nest. Connections are via multi-conductor, insulated cable. The recorder, thermistor and relay are powered by one or two 12 VDC batteries; the clock and camera are driven by rechargeable 1.5 VDC dry cells.

Detectors may be operated independently or in concert. The presence of a bird at the nest is detected when the infrared beam is blocked by the bird's body. Interruption of the 5-mm diameter beam, projected from the lens of the relay to an 8-cm plastic reflector and back to the relay, closes the circuit between the relay and the interface, which, in turn, closes the circuit to the event channel of the recorder (Fig. 1). The interface (Fig. 2) is necessary because the infrared relay switching transistor has a maximum current limit of 120 mA and the minimum current needed to activate the event pen is 500 mA. When inserted in the egg air cell or nest, the thermistor monitors the bird's presence by recording cooling during an

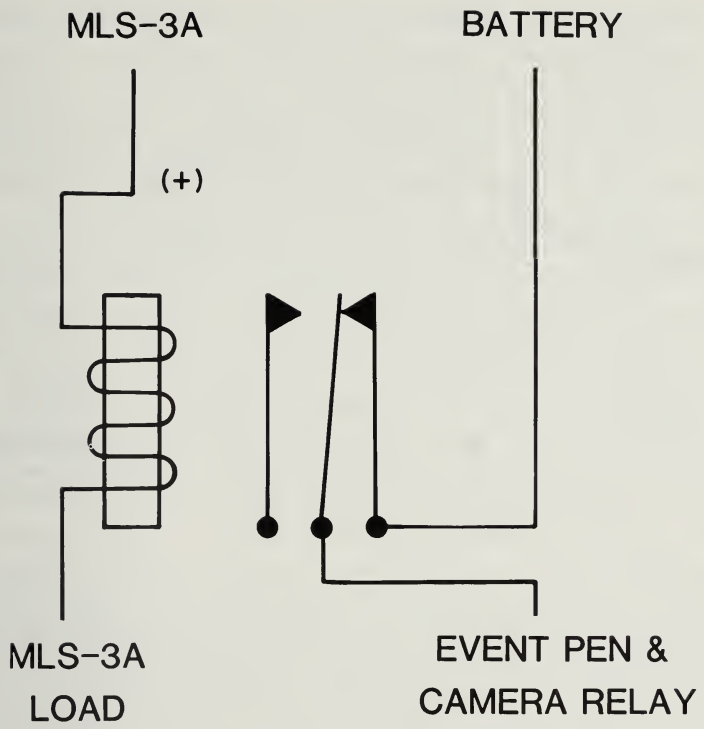


FIG. 2. Schematic diagram of infrared relay-recorder interface.

absence. In independent mode, the camera shutter is activated by an internal timer at preselected intervals over a range of 1–60 sec, recording on film the nest and its surroundings during daylight and by using a strobelight at night. In dependent mode, single frame exposures are triggered by interruption of the infrared beam so that the animal blocking the beam is photographed.

An independent time reference is needed for the recorder because the chart speed varies with the battery voltage, which is a function of power demand, battery condition and temperature. This is attained by opening briefly the thermistor circuit once an hour. A magnetic reed switch attached to the noon position of the clock with a small magnet glued to the minute hand provides an inexpensive but accurate reference.

Humid conditions may cause chart paper jamming. This can be prevented by encasing the recorder in an airtight case containing a noncorrosive desiccant ($CaSO_4$).

Field application.—The 12 VDC power supply permits monitoring in

remote locations and the cable connections allow maintenance of the recorder without disturbing the bird at the nest. Installation timing and configuration depend on the characteristics of the species being studied. A typical application entails locating a nest, preferably during the prelaying or early laying stages, and choosing or constructing a suitable site for the instrument case; placement of the relay, thermistor probe, camera or combination of these at the nest completes the process.

The infrared relay installation depends on the physical construction of the nest, the posture of the sitting bird, the size of target it provides and the substrate on which the nest is built. Nests constructed on stable substrate, e.g., most dabbling duck nests, present little difficulty. Two sharpened, metal angle-irons are driven into the soil on a line bisecting the nest cup and the relay is bolted to 1 stake, the reflector to the other. The infrared beam is adjusted by moving the relay and reflector vertically until the beam is broken by the sitting bird's body. The possibility that vegetation or nest materials will block the beam can be reduced by placing the relay and reflector as close as possible to the rim of the nest cup. In addition, small boards can be positioned between the nest cup and the relay and reflector to arrest growth of vegetation. Prior to installation exposed surfaces should be painted to match the colors at the nest-site. Relay installation at overwater nests with an unstable substrate, e.g., nests of most diving ducks, is accomplished by driving 2 metal rods into the marsh bottom. The relay and reflector are then attached to the rods and aligned in the same manner as in the case of a ground nest. When monitoring cavity nesting birds, the relay and reflector are fastened to brackets and aligned so that the bird interrupts the beam when entering or departing.

The thermistor probe is inserted into an egg using a technique similar to that of Caldwell and Cornwell (1975:709). The egg air cell is located with a flashlight and outlined on the egg shell with a pencil; a small (0.8 mm) hole is drilled in the shell at the apex of the air-cell end with a sterile bit, taking care not to perforate the air-cell membrane, and the hole is enlarged with a sterile scalpel to accommodate the thermistor. The probe, dipped in alcohol and allowed to dry, is inserted adjacent to the air-cell membrane and the hole sealed with epoxy glue (Fig. 3). The termistor wire is then taped to the long axis of the egg with adhesive tape. After inserting the probe, the egg is placed in the nest, the probe wire drawn through the bottom of the cup and out the side of the nest. For species in which the egg air cells are too small to accept the probe, e.g., Spotted Sandpiper (*Actilis macularia*), the probe may be glued to the side of an egg, placed in an artificial egg, or fastened to the bottom of the nest.

Unlike the silent, infrared relay, the camera emits a faint click when

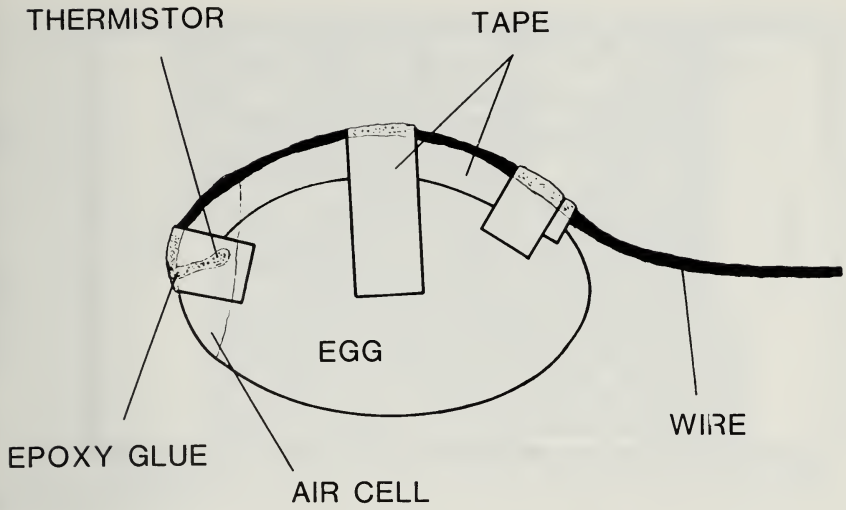


FIG. 3. Diagram of thermistor implantation in an egg.

the shutter releases. Thus, the camera and tripod must be positioned a sufficient distance from the nest to avoid frightening the bird. Because photographic monitoring in independent mode is not continuous, i.e., must be set at a 1–60 sec interval, selection of the shutter release rate is important. If the frequencies of brief activities, e.g., egg turning and preening on the nest, are to be measured, the interval must be less than the minimum duration of these behaviors. A clock placed in the field of view simplifies the film analysis.

For species monitored to date, a chart speed of 5 cm/h allowed measurement of periods on or off the nest to the nearest minute. Chart rolls are 19.2 m long, hence, a paper change is necessary every 15 days. A more rapid speed, attained by a simple and inexpensive gear change, would be necessary for accurate measurement of activities of shorter duration.

The frequency of battery change depends on the condition of the batteries, length of connecting sensor cables and temperature. Using the infrared relay, the thermistor and the camera in dependent mode with 33 m of cable, a single 65 A-h battery will provide power for 4 days; 2 batteries in parallel last 8 days. We found that changes at 2–4-day intervals are best. Replacement of the camera batteries with each film change reduces the possibility of power failure during a monitoring session.

Individual cables or a single multiconductor to the detectors may be used. Cables need not be shielded but must be waterproof and sufficiently durable to withstand months in the field. The infrared relay requires 3

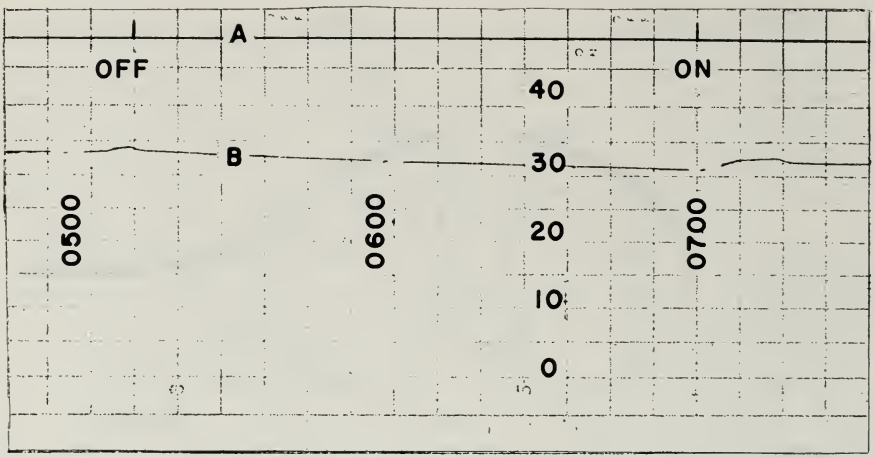


FIG. 4. Three-h recording of the activity of an incubating Wood Duck: (A) event channel showing departure from cavity at 05:16 (OFF) and return at 06:58 (ON) and (B) egg air cell temperature in °C. Breaks in B denote 1-h intervals.

conductors while the thermistor and camera 2 each. By cutting cables into 33 m lengths and using waterproof connectors, one may extend the cable needed to reach the nest from the recorder. The advantage of this is that the added power demand of the longer cable can be easily calculated. The battery must be changed 1 day sooner per 33 m of cable used. Thus, a monitor with two 33 m cable sections would require a battery change every 3 days vs 4 days for 1 with a single section. Cables at and near the nest should be secured by taping or tacking them down, then covered with vegetation or placed underwater.

EXAMPLES AND DISCUSSION

Species monitored employing components of the system include: the Trumpeter Swan (*Cygnus cygnus buccinator*), Canada Goose (*Branta canadensis*), Wood Duck (*Aix sponsa*), Pintail (*Anas acuta*), American Wigeon (*Anas americana*), Gadwall (*Anas strepera*), Green-winged Teal (*Anas crecca carolinensis*), Blue-winged Teal (*Anas discors*), Northern Shoveler (*Anas clypeata*), Lesser Scaup (*Aythya affinis*), Canvasback (*Aythya vallisneria*), Redhead (*Aythya americana*), Ring-necked Duck (*Aythya collaris*), Ruddy Duck (*Oxyura jamaicensis*), Western Grebe (*Aechmophorus occidentalis*), Spotted Sandpiper, Short-eared Owl (*Asio flammeus*) and Sharp-tailed Grouse (*Pedioecetes phasianellus*).

Based on data from 72 nests where the infrared relay and thermistor probe were employed, 32 of 1066 (3.0%) monitored days were lost due to

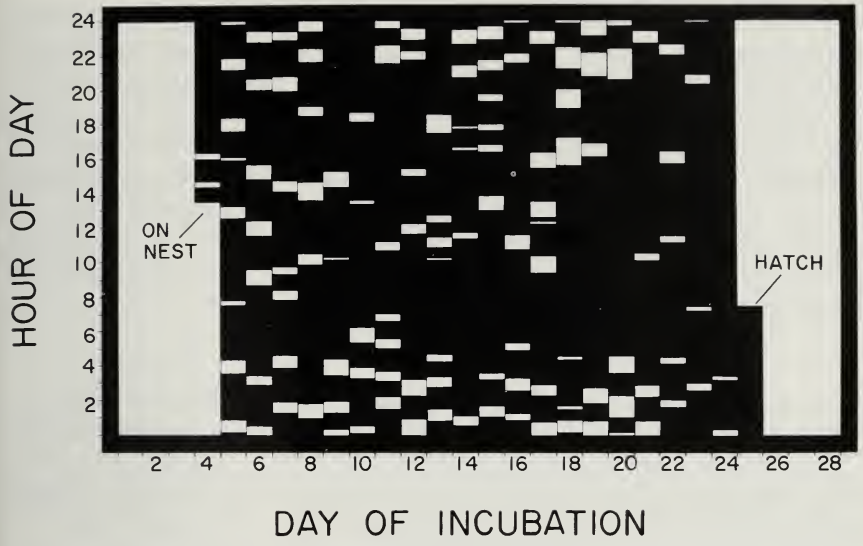


FIG. 5. Example of the nest attentiveness of a Ruddy Duck female, 3–27 June 1975, recorded using thermistor and infrared relay sensors.

sensor or recorder failure. Moreover, no records of inattentive and attentive periods at the nest were lost when using 3 sensors (N = 10 nests, 216 days). Statistical treatment of incubation time budget data is difficult without relatively complete records; therefore, keeping instrument failures to a minimum is important.

The multiple sensor approach not only permits recording of prelaying, laying and incubation time budgets, it also allows synchronous measures of egg air cell and/or nest air temperature and parent bird postures, displays, preening, sleep and other activities at the nest. An example of the recorder output for a Wood Duck recess is given in Fig. 4, and for a Ruddy Duck incubation attentiveness pattern in Fig. 5. Individuals frequenting a nest can be identified on film if markers or unique characters are present.

The cost of a unit with the 3 sensors is about $800 per monitor, and the construction is relatively simple. Except for the infrared relay, recorder, camera and thermistor, all components used in the system may be purchased in most electronic stores. A knowledge of simple DC parallel and series circuits is needed to assemble or repair the interface and time-reference circuits.

The system may have minor disadvantages when used to monitor birds that are disturbed by the thermistor wire attached to the egg or nest, or by changing of the camera film and batteries. We have not encountered

the former and have found that 84.1% (N = 44) of the eggs with implanted thermistors have hatched. We suspect that species such as raptors may be difficult to monitor using the thermistor (see Varney and Ellis 1974). But the camera and infrared sensor would provide data in these cases. When the camera must be placed so close to the nest that the sitting bird is disturbed during maintenance, the infrared and thermistor recordings must be carefully studied and the film and batteries changed when the bird is off the nest. This may be done for non-continuous incubating species but not for one in which both sexes incubate or others whose nest is constantly attended.

SUMMARY

The construction and field application of a multiple sensor (photoelectric-thermistor-photographic) system for avian nesting studies is described. The portable, battery-powered system has several advantages over previously described techniques. Foremost is the accurate and continuous recording of incubation time budgets. The system permits synchronous recordings of egg air cell and/or nest air temperature, postures, displays, preening, nest construction, and prelaying and incubation time budgets.

ACKNOWLEDGMENTS

We thank William H. Marshall and Milton W. Weller, Dept. Entomology, Fisheries and Wildlife, University of Minnesota, for reviewing the manuscript. John D. Afton assisted with the electrical design. Financial support was provided by the Graduate School and Minnesota Agricultural Experiment Station, University of Minnesota and the Delta Waterfowl Research Station, Portage La Prairie, Manitoba. This paper is No. 10,939 of the Scientific Journal Series of the Minnesota Agricultural Experiment Station.

LITERATURE CITED

Baldwin, S. P. and S. C. Kendeigh. 1927. Attentiveness and inattentiveness in the nesting behavior of the House Wren. Auk 44:206–216.

Caldwell, P. J. and G. W. Cornwell. 1975. Incubation behavior and temperatures of the Mallard Duck. Auk 92:706–731.

Drent, R. 1970. Functional aspects of incubation in the Herring Gull (*Larus argentatus*). Behaviour Suppl. 17:1–132.

Farner, D. S. 1958. Incubation and body temperatures in the Yellow-eyed Penguin. Auk 75:249–262.

Gilmer, D. S., V. B. Kuechle and I. J. Ball. 1971. A device for monitoring radio-marked animals. J. Wildl. Manage. 35:829–832.

Holstein, V. 1942. Duehogen, *Astur gentilis dubivs* (Sparrman). Biol. Stud. over Danske Rovfugle. I (Copenhagen).

Huggins, R. A. 1941. Egg temperatures of wild birds under natural conditions. Ecology 22:148–157.

Kendeigh, S. C. 1952. Parental care and its evolution in birds. Illinois Biol. Monogr. 22:148–157.

Kessler, F. 1962. Measurement of nest attentiveness in the Ring-necked Pheasant. Auk 79:702–705.

Kossack, C. W. 1947. Incubation temperatures of Canada Geese. J. Wildl. Manage. 11:119–126.

Miller, K. J. 1976. Activity patterns, vocalization, and site selection in nesting Blue-winged Teal. Wildfowl 27:33–43.

Norton, D. W. 1972. Incubation schedules of four species of calidridine sandpipers at Barrow, Alaska. Condor 74:164–176.

Pulliainen, E. 1978. Behavior of a Willow Grouse *Lagopus l. lagopus* at the nest. Ornis Scand. Fenn. 55:141–148.

Skutch, A. F. 1962. The constancy of incubation. Wilson Bull. 74:115–152.

Snelling, J. C. 1972. Artificial incubation of Sparrow Hawk eggs. J. Wildl. Manage. 36:1299–1304.

Varney, J. R. and D. J. Ellis. 1974. Telemetering egg for use in incubation and nesting studies. J. Wildl. Manage. 38:142–148.

Weeden, J. S. 1966. Diurnal rhythm of attentiveness of incubating female Tree Sparrows (*Spizella arborea*) at a northern latitude. Auk 33:368–388.

Weller, M. W. and D. V. Derksen. 1972. Use of time-lapse photography to study nesting activities of birds. Auk 89:196–200.

Dept. entomology, fisheries and wildlife, univ. minnesota, st. paul, minnesota 55108. (present address ada: delta waterfowl research station, portage la prairie, manitoba r1n 3a1 canada). accepted 15 jan. 1981.

THE INTERNATIONAL OSPREY FOUNDATION, INC.

The International Osprey Foundation, Inc. (TIOF), a non-profit organization, has been formed to study the problems of restoring Osprey numbers to a stable population, make recommendations to enhance the continued survival of the Osprey and initiate education programs. Based on Sanible Island, Florida, TIOF monitors Osprey nests on the island and is responsible for an artificial nesting program already established there. A computerized list of Osprey researchers and a working bibliography are being compiled. For further information write: Mark A. Westall, President TIOF, 289 Southwinds, Sanibel, Florida 33957.

Wilson Bull., 93(3), 1981, pp. 334–339

FORAGING SPEEDS OF WARBLERS IN LARGE POPULATIONS AND IN ISOLATION

Douglass H. Morse

Earlier, I (Morse 1968) demonstrated that during the middle of the breeding season female spruce-woods warblers (*Dendroica* spp.) foraged significantly faster than did their mates, a pattern subsequently reported in a number of other warblers (e.g., Black 1975, Sherry 1979). I attributed this difference to the females performing all of the incubation and a majority of the feeding of newly-hatched young, thus putting their foraging time at a premium. Data subsequently gathered on nearby island isolates of the same populations of 2 species (Morse 1971, 1977), combined with data on standing crops of insects in both mainland and island forests (Morse 1976a, 1977), make it possible to assess foraging speeds of Black-throated Green (*Dendroica virens*) and Yellow-rumped (*D. coronata*) warblers further.

Data on insect standing crops provide a common yardstick between the mainland and island populations. Their analysis suggests that no significant differences occur between the mainland and island areas except at the end of the season (Morse 1976a, 1977). Although standing crops may be imperfect indicators of productivity (e.g., Southwood 1966), insect faunas are similar on the islands and adjacent (shoreline) mainland plots (unpubl. data), and conditions influencing productivity (weather, etc.) are probably similar also. Therefore, the assumption of similarity in food availability seems reasonable. Given the limited foraging time available to all females and the high speeds at which mainland females forage at certain times, availability of insect food may be a critical factor at these times.

The islands studied differ from the mainland in that only 1 pair of any spruce-woods warbler species is present. Of 2 common nest predators on the mainland, the red squirrel (*Tamiasciurus hudsonicus*) is absent and the Blue Jay (*Cyanocitta cristata*) rarely visits. Both of these factors might lower the demands of nest attendance on females. Similarly, the absence of conspecifics might lower the demands for territorial proclamation and defense by the males. Male Black-throated Green Warblers sing considerably less on these islands than on the mainland (Morse 1970).

Given the apparent similarity in resource availability on the mainland and islands, the tendency for foraging speeds to fluctuate (Morse 1968), and the lessened demands on these individuals, one would predict island females involved with nesting activities to forage slower than mainland females. It is equivocal whether island males will forage slower than main-

land males when females are performing most of the nesting activities, since mainland males do not appear stressed in their foraging during this part of the cycle (Morse 1968). However, one would predict island males to forage substantially slower than mainland males when they are making major contributions to feeding fledged or nearly-fledged young.

STUDY AREAS AND METHODS

The "mainland" data were gathered on Hog Island (Todd Wildlife Sanctuary), Bremen, Lincoln Co., Maine. This is a large island of 132 ha covered by a mature red (*Picea rubens*) and white (*P. glauca*) spruce forest. It is separated from the mainland proper by a narrow channel, and its species composition is similar to that of the adjacent mainland (Morse 1976a). This forest is described in detail elsewhere (Morse 1968, 1976a, and references therein). The island data were gathered on 6 small nearby islands with spruce forests ranging from 0.35–1.50 ha. These islands are Crow and Jim's islands, Bremen, Lincoln Co.; Indian and Thief islands, Bristol, Lincoln Co.; and Ram and Crane islands, Friendship, Knox Co., Maine. They are described in detail elsewhere (Morse 1971).

Data on foraging speeds of island birds were gathered as described by Morse (1968). Briefly, in addition to data gathered on foraging sites (reported in Morse 1968, 1971), I scored birds for their rapidity of foraging movement. The scoring technique was adopted because individuals often became temporarily obscured in foliage so thick that detailed beak movements could not be observed, although rate of overall progress could nevertheless be ascertained accurately. This method was checked regularly on birds at sites where frequency of foraging could be observed closely. The following scores were used: 1 = 1–2 pecks/min, 2 = 3–4, 3 = 5–6, 4 = 7–9, 5 = 10–12, 6 = 13–15, 7 = 16–20, 8 = 21–25, 9 = 26–30, 10 = 31+.

The data on mainland foraging speeds were reported earlier (Morse 1968), and those from the islands were obtained during 1967–1969 while foraging data (Morse 1971) were being gathered. Analyses of insect standing crops were not available when the 2 foraging papers were prepared (Morse 1968, 1971), but were published later (Morse 1976a, 1977).

At least 12 pairs of each island and mainland group of warblers were studied, except island Black-throated Green Warblers, for which the sample consisted of 8 pairs. Each point in Fig. 1 represents observations at 10–200+ foraging sites.

Sampling of insects was carried out on the islands during the summers of 1968–1970, overlapping the period that foraging data were gathered. Insect sampling on the mainland was carried out during the summers of 1969–1972 and the mainland foraging data were gathered during the summers of 1966–1967. Since no noticeable insect outbreaks took place in the mainland forests during 1966–1967 and 1969–1972, and since rather similar arthropod biomasses occurred there during 1969–1972 (see Morse 1976a: Fig. 5a), I am proceeding under the assumption that the foraging of mainland birds was carried out under arthropod density regimes similar to those encountered during the summers of 1969–1972. Although I consider this to be a reasonable assumption, the reader should be aware of it, since insect outbreaks are not uncommon in forests and may have a marked effect on both the foraging patterns and abundance of insectivorous birds (e.g., Holmes and Sturges 1975, Morse 1978).

RESULTS

Foraging speeds of warblers are represented in Fig. 1, and significance levels between mainland and island individuals of the same species and

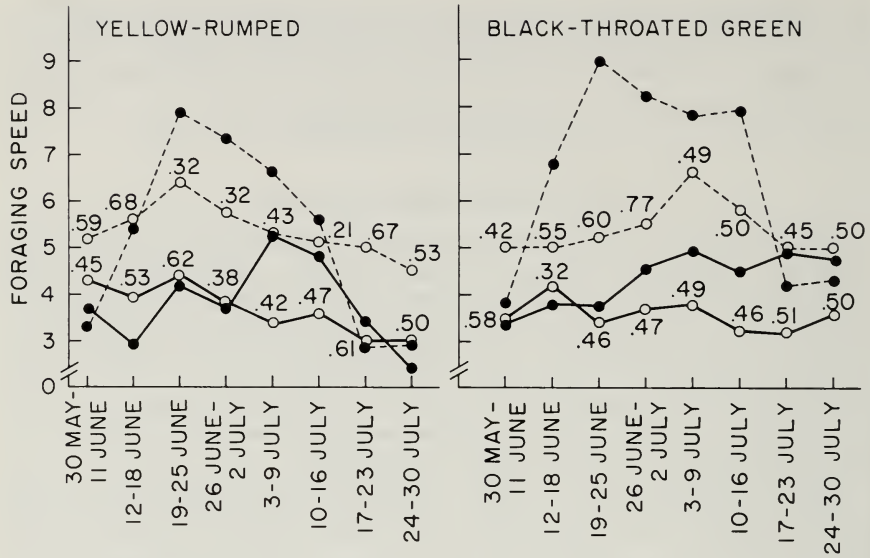


FIG. 1. Mean foraging speeds of male (solid line) and female (dashed line) warblers. Filled circles = mainland and open circles = islands. Mainland data points from Morse (1968). Standard deviations accompany each data point from an island. Standard deviations from mainland data points are published in Morse (1968, Fig. 5).

sex in Table 1. During the middle of the season, island females of both species foraged significantly more slowly than did mainland females. This period coincides with the time during which they incubate and feed young still in the nest (Palmer 1949; Morse 1968, unpubl. data). No significant differences in foraging speeds of females occurred immediately before this, the nest-building period, or at the end of the season, after young had left their nests. Island females of both species did, however, forage significantly faster at the very beginning of the season, which includes the period during which they search for nest-sites and accumulate resources for egg production. Only then did either island males or females forage significantly faster than their mainland counterparts (Table 1).

Island males of both species foraged significantly more slowly than mainland males during the middle of the season, a time coinciding with the first appearance of fledged young. This pattern held through the end of the season in Black-throated Green Warblers, but disappeared at the very end of the season in Yellow-rumped Warblers.

Island females always foraged faster than island males (Fig. 1), a difference that was statistically significant ($P < 0.05$ or less in 1-tailed Mann-Whitney U-tests) in all but 2 cases: 30 May–11 June for the Yellow-rumped

TABLE 1

LEVELS OF SIGNIFICANCE FOR DIFFERENCES IN FORAGING SPEEDS BETWEEN MAINLAND AND ISLAND WARBLERS[a]

Date	Species and sex			
	Black-throated Green Warbler		Yellow-rumped Warbler	
	Male	Female	Male	Female
30 May–11 June	>0.05 (47, 217)	<0.001[b] (43, 38)	>0.05 (25, 133)	<0.001[b] (12, 69)
12–18 June	>0.05 (15, 132)	>0.05 (18, 35)	>0.05 (12, 192)	>0.05 (29, 72)
19–25 June	>0.05 (34, 43)	<0.001 (20, 12)	>0.05 (74, 92)	<0.001 (18, 33)
26 June–2 July	>0.05 (89, 61)	<0.001 (10, 21)	>0.05 (54, 105)	<0.001 (14, 52)
3–9 July	<0.01 (90, 49)	<0.05 (17, 75)	<0.05 (35, 115)	<0.001 (13, 56)
10–16 July	<0.001 (161, 12)	<0.001 (43, 16)	<0.05 (67, 108)	>0.05 (52, 34)
17–23 July	<0.025 (134, 18)	>0.05 (14, 14)	<0.025 (79, 77)	>0.05 (27, 16)
24–30 July	<0.05 (126, 10)	>0.05 (37, 17)	>0.05 (26, 29)	>0.05 (16, 13)

[a] Number of observations in parentheses, with mainland birds preceding comma and island birds following comma.
[b] Island foraging speed faster than mainland foraging speed. In all other significant differences, mainland birds foraged faster than island birds; 1-tailed Mann-Whitney *U*-tests; *U*'s supplied by author upon request.

Warbler and 12–18 June for the Black-throated Green Warbler (Table 1). Both of these periods preceded the incubation stage of most individuals.

Foraging speeds of the 2 species shifted strikingly in concert over the season, greatly strengthening confidence in this analysis. In 7 of the 8 time periods island male Black-throated Green Warblers and island male Yellow-rumped Warblers simultaneously foraged significantly slower than did their mainland equivalents, or foraging speeds of these island and mainland birds were simultaneously not significantly different (Table 1) (P = 0.035, N = 8, in a 1-tailed binomial test). Results for females of the 2 species also corresponded in the same way during 7 of the 8 time periods (P = 0.035, N = 8), with the only difference being that in the first time period island females of both species foraged significantly faster than their mainland equivalents.

DISCUSSION

In that climatic factors and food availability were apparently similar on island and mainland study areas, most of these results may be attributed to differences in interference by other individuals and/or differences in danger of nest predation. Since no experiments were performed it is not possible to distinguish unequivocally between the alternatives, but strong inferences can be made.

Differences between island and mainland males can be tentatively attributed to levels of interference or potential interference, since the males make no contribution to incubation and little to new-born young (Morse

1968). Amounts of stationary singing by Black-throated Green Warblers were strikingly lower on islands during the middle of the season (Morse 1970) and, judging subjectively, a similar pattern seemed to hold for the Yellow-rumped Warbler as well. The stationary song of the Black-throated Green Warbler is given from prominent locations and seems associated with territorial display (Morse 1967, 1970). The slower foraging speed of the island males was thus probably a consequence of a modified time budget resulting from a decrease in frequency of stationary singing.

Differences in habitat use are unlikely to account for the differences in foraging speed of male Black-throated Green Warblers, since they used the same parts of both mainland and island vegetation (Morse 1971). Although island-dwelling Yellow-rumped Warblers did change their habitat use from that on the mainland (Morse 1971), the close parallels of their foraging speeds with those of the Black-throated Green Warblers mitigates against this shift being a major factor in the differences of their foraging speeds.

Differences in frequencies of interactions are unlikely to account for the differences in foraging speeds of mainland and island female warblers during the middle of the season, however. Even on the mainland only infrequent interactions were observed between females and other individuals (Morse 1976b) and mainland females' activities off the nest consisted almost entirely of extremely rapid foraging (Morse 1968).

The virtual absence of nest predators on these islands may be a more important factor affecting the foraging speed of females. Brood destruction is high where nest predators are common (Skutch 1976), and release from it could affect activity patterns strikingly. Unfortunately, I do not have comparative information on the attentiveness of females at island and mainland nests. However, attentiveness at mainland nests was extremely high, with these birds foraging for only short periods (Morse 1968). The greater ease that I experienced in observing island females (Morse 1971) suggests that they spent greater amounts of time off their nests than did mainland females. If correct, this interpretation means that attendance patterns of these warblers are only partially governed by thermoregulatory considerations and that the birds in question can adjust their attendance regimes in response to the presence or absence of nest predators about them. Current reviews of incubation behavior, oriented toward thermoregulatory aspects, make slight reference to pressures from nest predators as a possible modifier of attendance regimes at the nest (Ricklefs 1974, White and Kinney 1974).

I have no explanation for the greater foraging speeds of island females of both species at the very beginning of the season. Insect crops at that time were virtually identical, though variable, in the 2 areas (Morse 1977).

These were the only cases in which island birds foraged faster than their mainland counterparts.

SUMMARY

Male and female Black-throated Green and Yellow-rumped warblers isolated from conspecifics and nest predators on small islands foraged more slowly during the height of the breeding season than did ones in large mainland populations. Since food supplies on mainland and island were similar, differences between males are interpreted to result from a decrease in stationary singing associated with territorial maintenance, those between females a consequence of decreased nest attentive behavior associated with nest predators.

ACKNOWLEDGMENTS

I thank R. T. Holmes for comments on the manuscript. This work was partially supported by the National Science Foundation (GB-3226, GB-6071, GB-31005).

LITERATURE CITED

Black, C. P. 1975. The ecology and bioenergetics of the Northern Black-throated Blue Warbler (*Dendroica caerulescens caerulescens*). Ph.D. diss., Dartmouth Coll., Hanover, New Hampshire.

Holmes, R. T. and F. W. Sturges. 1975. Bird community dynamics and energetics in a northern hardwoods ecosystem. J. Anim. Ecol. 44:175–200.

Morse, D. H. 1967. The contexts of songs in Black-throated Green and Blackburnian warblers. Wilson Bull. 79:64–74.

———. 1968. A quantitative study of foraging of male and female spruce woods warblers. Ecology 49:779–784.

———. 1970. Territorial and courtship songs of birds. Nature 226:659–661.

———. 1971. The foraging of warblers isolated on small islands. Ecology 52:216–228.

———. 1976a. Variables affecting the density and territorial size of breeding spruce-woods warblers. Ecology 57:290–301.

———. 1976b. Hostile encounters among spruce-woods warblers (*Dendroica*, Parulidae). Anim. Behav. 24:764–771.

———. 1977. The occupation of small islands by passerine birds. Condor 79:399–412.

———. 1978. Populations of Bay-breasted and Cape May warblers during an outbreak of the spruce budworm. Wilson Bull. 90:404–413.

Palmer, R. S. 1949. Maine birds. Bull. Mus. Comp. Zool. 102:1–656.

Ricklefs, R. E. 1974. Energetics of reproduction in birds. Publ. Nuttall Ornithol. Club 15:152–297.

Sherry, T. W. 1979. Competitive interactions and adaptive strategies of American Redstarts and Least Flycatchers in a northern hardwoods forest. Auk 96:265–283.

Skutch, A. S. 1976. Parent birds and their young. Univ. Texas Press, Austin, Texas.

Southwood, T. R. E. 1966. Ecological methods. Methuen, London, England.

White, F. N. and J. L. Kinney. 1974. Avian incubation. Science 186:107–115.

DIV. BIOLOGY AND MEDICINE, BROWN UNIV., PROVIDENCE, RHODE ISLAND 02912. ACCEPTED 16 OCT. 1980.

Wilson Bull., 93(3), 1981, pp. 340–349

DIFFERENTIAL PASSERINE DENSITY AND DIVERSITY BETWEEN NEWFOUNDLAND AND OFFSHORE GULL ISLAND

Monique I. Vassallo and Jake C. Rice

Characteristically, islands have impoverished biotas (MacArthur and Wilson 1963, 1967; Diamond 1975; many others). Several reasons have been proposed to account for this depauperate condition. Remoteness of the island (MacArthur and Wilson 1963, 1967; Simberloff and Wilson 1969) and island size (Diamond 1975, MacArthur and Wilson 1967, Power 1976) can both affect the equilibrium number of species, either directly or indirectly, with small, remote islands having the fewest species. The potential reduction of habitat diversity on small islands may also indirectly lead to increased interspecific competition, and consistent with the competitive exclusion principle, a reduction in number of species may result through loss of close competitors (Grant 1966a, MacArthur and Wilson 1967, Morse 1971). Other indirect effects of island size, isolation or topography have been proposed as factors determining equilibrium numbers of species on islands (MacArthur et al. 1973, Morse 1971). Few of the above notions have escaped some criticism (e.g., Grant 1966a, Lynch and Johnson 1974).

Differences in numbers of species often occur concomitantly with changes in the density of island avifaunas. Increases in density commonly occur and are usually attributable to an increase in the density of a few species, relative to their mainland densities (Crowell 1961, Grant 1966b, MacArthur et al. 1972). However, lower net densities of island avifaunas have also been reported. These have been attributed to species expanding into suboptimal habitat where they occur in lower densities (Diamond 1970), to deterioration of the local gene pool (Diamond 1970), or to simply a decrease in species richness without a concomitant increase in densities of remaining species (MacArthur et al. 1972, Yeaton and Cody 1974).

Species also differ in their abilities to colonize small islands, making it possible in some instances to predict systematically the order of colonization of island chains, knowing the likely source population (Morse 1971, Diamond 1975, Terborgh et al. 1978). A consequence of this differential colonization ability of bird species is that an island adjacent to another island will have a different reservoir of potential colonizers than an island directly offshore from a continental land mass. The island source community ought to be one already selected for colonization ability, as has been found by Terborgh and Faaborg (1973) and Terborgh et al. (1978).

Another well-known biogeographical phenomenon is the decline of species diversity and richness with increasing latitude and/or harshness of climate (Klopfer and MacArthur 1960, 1961; Rotenberry 1978). The proportion of the community made up of nonpasserines also declines with increasing latitude (Klopfer and MacArthur 1960). Most studies of island biogeography have been conducted in tropical or warm temperate latitudes. The few studies farther north have considered only a few taxa (Morse 1971, but see Morse 1977, Cody and Cody 1972).

Newfoundland is a large island off the coast of eastern Canada. It shows a markedly depauperate avifauna, relative to adjacent Nova Scotia and Gaspé, Quebec (Peters and Burleigh 1951, Godfrey 1966). For example, Godfrey (1966) shows that over a quarter of the species breeding in Nova Scotia do not breed in Newfoundland, although recent records may alter that figure slightly. Gull Island (47°15′N, 52°46′W) is a small island off the east coast of Newfoundland, in the Witless Bay Seabird Sanctuary. This study examined the species diversity, richness and density of the land birds on Gull Island, to see if the low species richness of Newfoundland itself influenced the degree or pattern of species change between Gull Island and the adjacent coast of Newfoundland.

METHODS

Study area.—Gull Island, in the Witless Bay Seabird Sanctuary, comprises 0.95 km² and is 1.6 km from the nearest point of land (Fig. 1). Open grassy areas occur along the shore in which there are large numbers of nesting burrows of Common Puffins (*Fratercula arctica*). Inland mature boreal forest with balsam fir (*Abies balsamea*), white spruce (*Picea glauca*) and white birch (*Betula papyrifera*) predominate. Dead trees are common and there are bogs.

South Head, Witless Bay (47°17′N, 52°47′W) was the adjacent mainland area studied. Grassy fields and bogs were more abundant here than on Gull Island. Forested areas were comparable in species composition, but younger due to cutting. The 2 areas lie within the boreal forest region of Rowe (1972).

The vegetation of the 2 areas was compared quantitatively and reported with a detailed comparison of the ecological differences between sites for selected avian species (Vassallo and Rice, in press). Briefly, the South Head forest had fewer large dead trees and the most densely vegetated areas were denser than any on Gull Island. The trees in these exceptionally dense areas were mostly black spruce (*P. mariana*), which were more abundant on South Head than on Gull Island. White birch was more common on Gull Island. However, all habitat types were present at both sites and differences were of quantitatively extreme densities, not qualitative attributes.

Census methods.—Line transects were established at both localities along preexisting pathways (Fig. 2). Transects on the island and mainland measured 1.44 and 1.62 km, respectively. Both transects traversed open and forested areas, and although open areas were more abundant at South Head than Gull Island, lines at South Head were oriented so that comparable amounts of each habitat were censused. Censuses began within 1 h of sunrise and data from

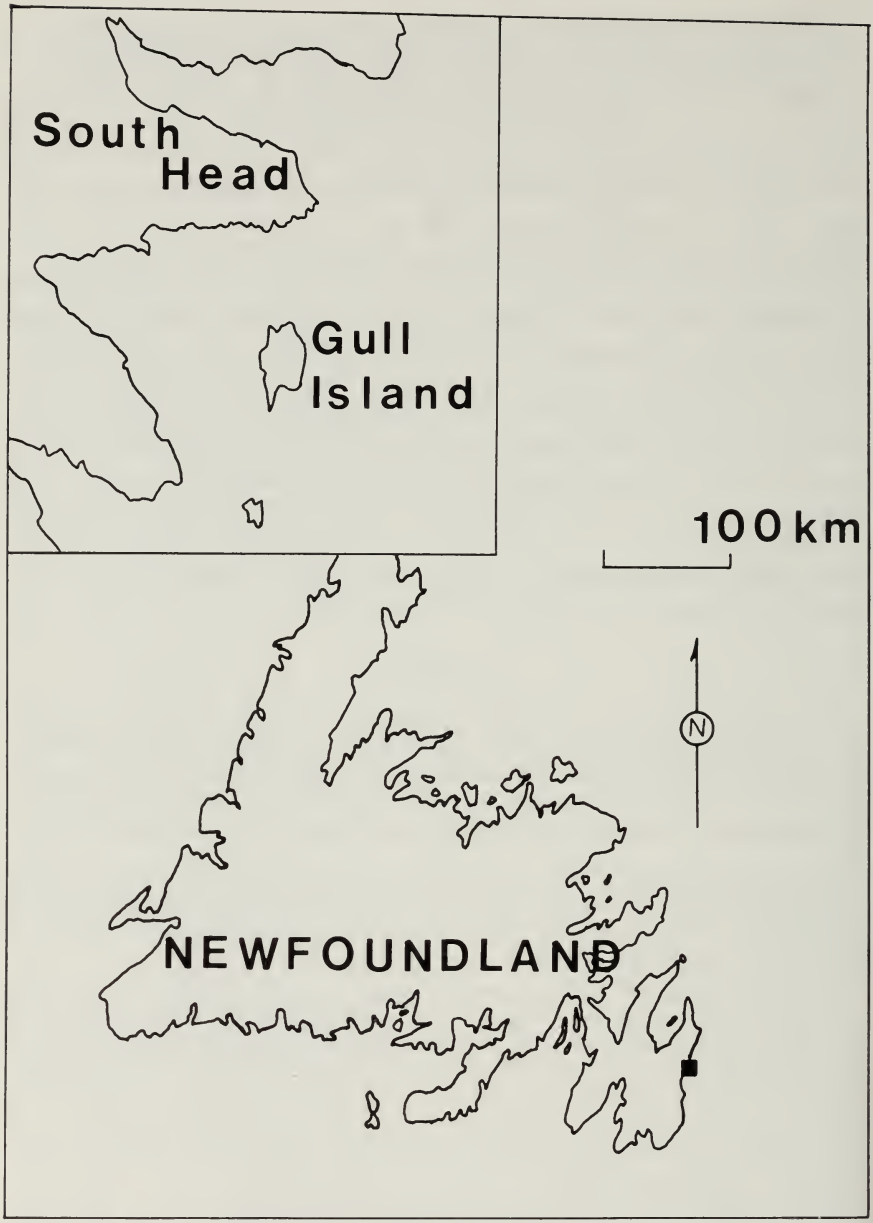


FIG. 1. Map of the island of Newfoundland, showing the location of the study area on the Avalon Peninsula. The inset shows Gull Island and South Head, Witless Bay.

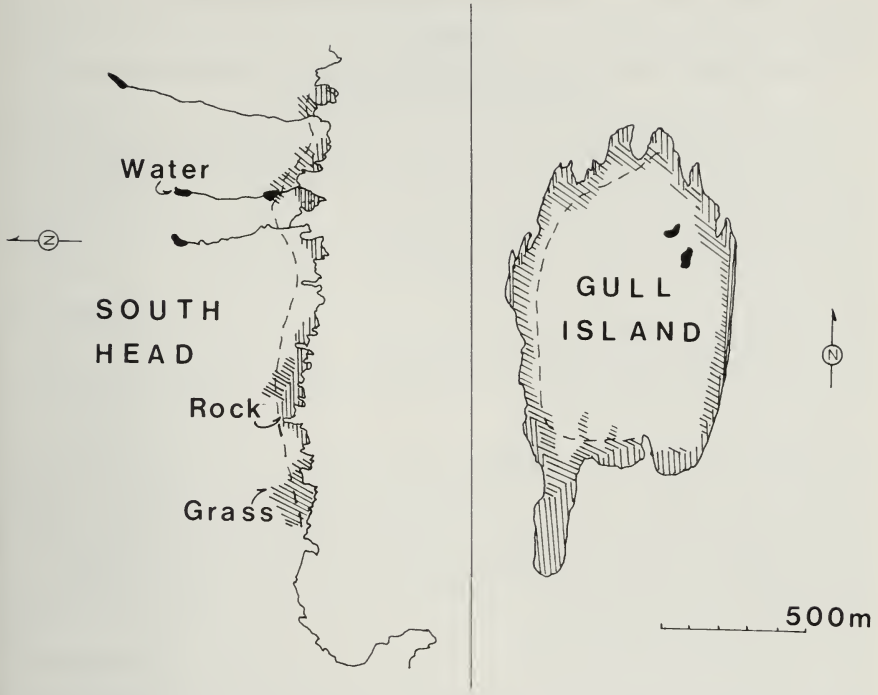


FIG. 2. Map of the 2 areas, showing major topographic features. The broken lines indicate the transect lines, vertical barring areas of exposed rock, slanted barring areas of grassy meadow, black areas open fresh water and all unshaded land areas are boreal forest.

censuses interrupted by inclement weather were discarded. Thirty censuses were done at South Head between 18 May and 19 July 1977, and 11 on Gull Island between 16 June and 26 July. Additional species seen at other times of day are considered in the comparisons of species richness, but not in the calculations of density or diversity measures.

Analyses.—Diversity indices were calculated for all censuses, using Shannon's Index (Pielou 1966a, b). Because the underlying distribution is unknown, a Kruskal Wallis test (Sokal and Rohlf 1969) was used to compare diversity indices between sites.

Bird densities were calculated for each census day as birds per km of line transect. No attempt was made to weight density by proximity to the line transects, because of greatly different patterns of species detectability between habitat types. To compare monthly and seasonal densities between areas we used *t*-tests of $\log_{10}$ of the abundance measures, after testing for homogeneity of variances. For species common at both sites, individual species densities were compared in the same way. However, densities were first compared within each site between June and July, and data for the 2 months were not combined if abundances changed significantly between months.

RESULTS

Thirteen species of passerines were observed on Gull Island, whereas 25 species were seen on South Head (Table 1). Eleven species were com-

Table 1

Passerine Birds Observed on South Head or Gull Island During Morning Censuses (X) or Other Times (T)

Species	South Head	Gull Island
Eastern Kingbird (*Tyrannus tyrannus*)	X[a]	
Yellow-bellied Flycatcher (*Empidonax flaviventris*)	X	X
Common Crow (*Corvus brachyrhynchos*)	X	
Common Raven (*Corvus corax*)	T[a]	X
Black-capped Chickadee (*Parus atricapillus*)	X	
Boreal Chickadee (*P. hudsonicus*)	X	X
Red-breasted Nuthatch (*Sitta canadensis*)	X[a]	
Brown Creeper (*Certhia familiaris*)		X[a]
Winter Wren (*Troglodytes troglodytes*)		X
American Robin (*Turdus migratorius*)	X	X
Gray-cheeked Thrush (*Catharus minimus*)	X	X
Golden-crowned Kinglet (*Regulus satrapa*)	X[a]	
Starling (*Sturnus vulgaris*)	X[a]	
Northern Parula (*Parula americana*)	T[a]	
Blackpoll Warbler (*Dendroica striata*)	X	X
Northern Waterhrush (*Seiurus noveboracensis*)	X	X
Wilson Warbler (*Wilsonia pusilla*)	X	
Rusty Blackbird (*Euphagus carolinus*)	T[a]	
Pine Grosbeak (*Pinicola enucleator*)	X	X
Pine Siskin (*Carduelis pinus*)	X	X
Red Crossbill (*Loxia curvirostra*)	X	
White-winged Crossbill (*Loxia leucoptera*)	X	X
Savannah Sparrow (*Passerculus sandwichensis*)	X	
Dark-eyed Junco (*Junco hyemalis*)	X	
White-throated Sparrow (*Zonotrichia albicollis*)	X	
Fox Sparrow (*Passerella iliaca*)	X	X
Swamp Sparrow (*Melospiza georgiana*)	X	

[a] Not seen more than twice during summer.

mon to both sites, 2 others were recorded only on the island and 14 were recorded only on South Head. With the exception of the Brown Creeper (*Certhia familiaris*), all rarely encountered species were recorded at South Head rather than Gull Island. Not all species restricted to South Head were rare ones, however, as 8 species frequently seen there were never seen on Gull Island.

One striking difference between the avifaunas of South Head and Gull Island was the number of congeners present. At South Head 2 species of *Parus*, 2 of *Loxia* and 2 of *Corvus* were recorded, whereas on Gull Island only 1 species of each genus was present. Furthermore, at South Head 5 species of sparrows and juncos and 4 species of warblers were noted, but

TABLE 2

MONTHLY MEAN BIRD SPECIES DIVERSITIES AND DENSITIES FOR SOUTH HEAD AND GULL ISLAND FOR SUMMER 1977

	Diversity		Density (birds/km)		
	$\bar{x} \pm SD$	Range	$\bar{x} \pm SD$	Range	N
South Head					
June	3.323 ± 0.836	2.983–3.749	37.2 ± 1.22	28.5–51.8	15
July	3.617 ± 0.843	3.345–4.278	41.1 ± 1.19	35.2–47.5	7
Gull Island					
June	2.819 ± 0.171	2.677–2.895	31.5 ± 1.36	19.4–43.7	5
July	2.446 ± 0.236	2.330–2.615	27.6 ± 1.20	22.2–36.8	6

on Gull Island only 1 sparrow and 2 warblers were recorded. The decreased number of species on Gull Island results from a loss of taxonomically related species, rather than the complete loss of certain higher taxa or ecological guilds. As with richness, South Head species diversity was significantly higher than species diversity on Gull Island ($P < 0.005$, Table 2).

Total densities of birds did not differ between June and July at either Gull Island ($t = 0.889$, df = 9, NS) or South Head ($t = 1.125$, df = 20, NS; Table 2). There was a significantly higher density of birds per km at South Head than on Gull Island ($t = 3.458$, df = 31, $P < 0.01$). When densities of individual species are compared between sites a number of differences appear. American Robins (*Turdus migratorius*) and Blackpoll Warblers (*Dendroica striata*) have significantly higher densities at South Head, whereas Northern Waterthrushes (*Seiurus noveboracensis*), Boreal Chickadees (*Parus hudsonicus*) and Gray-cheeked Thrushes (*Catharus minimus*) have higher densities on Gull Island. In fact, for June, the density of Boreal Chickadees on Gull Island was significantly greater than the combined density of both chickadee species at South Head ($t = 2.220$, df = 18, $P < 0.05$), although the difference was not present in July ($t = 0.366$, df = 11, NS).

DISCUSSION

Consistent with contemporary theory, Gull Island had a lower number of species and a lower species diversity than did the adjacent mainland area. The species that were missing were a nonrandom subset of the South Head avifauna. On South Head 19 of 25 species recorded had a congeneric or close confamilial species present. On Gull Island only 5 species had

TABLE 3
MEAN DENSITIES AND SD OF INDIVIDUAL SPECIES AT EACH LOCALITY[a]

Species	South Head		Gull Island		"*t*" between sites (DF)
	June $\bar{x} \pm SD$	July $\bar{x} \pm SD$	June $\bar{x} \pm SD$	July $\bar{x} \pm SD$	
Fox Sparrow	5.79 ± 1.25	6.75 ± 1.23	5.81 ± 1.58	7.78 ± 1.85	1.38 (31)
Pine Siskin	4.50 ± 1.90	3.80 ± 2.16	4.43 ± 1.73	2.33 ± 1.72	1.58 (31)
American Robin	2.99 ± 1.29	2.56 ± 2.78	0.92 ± 1.34	0.99 ± 1.24	7.12 (31)***
Gray-cheeked Thrush	1.35 ± 1.56	1.86 ± 1.36	2.74 ± 1.20	3.32 ± 1.38	6.10 (31)***
Northern Waterthrush	4.27 ± 1.30	3.29 ± 1.24 2.30 (20)*	5.39 ± 1.45	7.39 ± 1.68	1.55 (18) June 3.76 (11) July**
Blackpoll Warbler	6.18 ± 1.39	5.61 ± 1.41	2.48 ± 1.39	0.99 ± 1.71 3.66 (9)**	5.89 (18) June** 7.06 (11) July**
Boreal Chickadee	2.28 ± 1.93	1.74 ± 1.80	6.45 ± 1.69	2.57 ± 2.00 2.42 (9)*	3.19 (18) June** 1.09 (11) July
Black-capped Chickadee	1.46 ± 1.51	1.45 ± 1.68			
Boreal and Black-capped chickadees	3.74	3.19	vs Boreal Chickadee		2.22 (18) June* 0.37 (11) July

[a] If monthly mean densities differed significantly within a site, "*t*-values and degrees of freedom are entered below the densities. Mean densities and standard deviations (SD) are birds/km of transect.
* $P < 0.05$; ** $P < 0.01$; *** $P < 0.001$.

close relatives present among the 11 shared species. The probability of randomly selecting 11 species from the South Head avifauna and having only 5 close taxonomic relatives is 0.014 (binomial test; the Emberizidae were separated by subfamily and all other divisions were at family level). Furthermore, the 2 species added to the Gull Island avifauna are both of families not recorded at South Head nor with other species present on Gull Island. Taxonomic closeness is commonly taken to imply some degree of ecological similarity and potential for competition (e.g., Emlen 1973:316). Therefore, these data support the notion that competitive ecological interactions play an important role in the dynamics of island biogeography, at least for small, nearshore islands (Morse 1971, 1977). The proximity of Gull Island to South Head and its relatively large size render isolation or inadequate island size unlikely explanations for the nonrandom change in species richness.

As with most other studies, it would be difficult to fully assess all effects

of habitat differences between Gull Island and South Head on bird species richness, density and diversity. The absence of pasture and small extent of bogs on Gull Island could account for the absence of Starlings (*Sturnus vulgaris*) and Swamp Sparrows (*Melospiza georgiana*), respectively, and the larger extent of windfallen trees and associated litter and undergrowth on Gull Island could account for the presence of the Winter Wren (*Troglodytes troglodytes*). Otherwise, the vegetational differences between the island and South Head are consistently differences in extremes of density reached by various plant taxa, rather than differences in overall habitat diversity or species composition (Vassallo and Rice, in press). Therefore, using habitat differences to account for the bird species distributions found here is only possible on a piecemeal, nonpredictive basis.

Although the total density of passerines on Gull Island was lower than at South Head, this difference does not appear to be simply a reflection of a lower habitat diversity on Gull Island. This density reduction did not reflect either an overall decline in numbers of each species, nor merely the effects of an uncompensated loss of some taxa. Some density differences, such as the increased density of Boreal Chickadees on Gull Island in the absence of the Black-capped Chickadee (*P. atricapillus*), are consistent with the notion of competitive release (MacArthur et al. 1972, MacArthur et al. 1973, Yeaton and Cody 1974). However, other species, e.g., the Gray-cheeked Thrush, also showed a significant increase in density, although 2 thrushes were present at both sites. Furthermore, the Blackpoll Warbler was exposed to fewer potentially competing canopy foragers and at least as much suitable habitat on the island but nonetheless had a lower density there.

Apparently, as with the effects of changing habitat diversity on bird species diversity and richness, the density effects of changes in the avian community do not follow a few rigorously predictable rules. The community dynamics are complex, and conditions in which density compensation and competitive release will occur are not universally specifiable.

In this study, we found a lower species diversity, a loss of close ecological and taxonomic relatives and a decrease in overall avian density on Gull Island. These effects were all observed, although the mainland area is itself an island showing substantial decreases in bird species richness and diversity relative to continental North America. The factors producing the difference in island fauna apparently do not merely filter once to produce an island fauna of good colonists ("supertramps" of Diamond 1975), but similar effects are produced through the community dynamics of colonization when the island itself becomes a source for another island (Terborgh and Faaborg 1973, Terborgh et al. 1978).

SUMMARY

Although the island of Newfoundland shows a characteristically depauperate avifauna relative to continental Maritime Canada, Gull Island, a small offshore island, has lower passerine species richness than does a nearby area of comparable habitat on the Newfoundland coast. The decrease from 25 to 13 species was due neither to the loss of all members of some higher taxa nor to completely stochastic species losses. Rather it reflected the reduction of groups of congeneric or confamilial species in the coastal area to single species represented on the island. Overall density compensation did not occur, and patterns of density difference of individual species showed some insular increases, some decreases, and some cases of no difference. Habitat differences between the sites account for much but not all of these avian community differences.

ACKNOWLEDGMENTS

Much of this work was completed while the first author was a M.Sc. student at Memorial University of Newfoundland, and was supported in part by a fellowship from the graduate school. Field and transportation expenses were provided by a National Research Council of Canada grant to the second author. Susan Noseworthy gave field assistance on Gull Island and Leonard Vassallo provided both field assistance and much appreciated support. Drs. D. Morse, P. Scott, D. Steele and W. Threlfall gave valuable comments on the thesis and/or this manuscript. Request reprints from J. C. Rice.

LITERATURE CITED

Cody, M. L. and B. B. J. Cody. 1972. Territory size, food density and clutch size in island wren populations. Condor 75:473–477.

Crowell, K. L. 1961. The effects of reduced competition in birds. Proc. Natl. Acad. Sci. U.S.A. 47:240–243.

Diamond, J. M. 1970. Ecological consequences of island colonization by Southwest Pacific birds. II. The effect of species diversity on total population density. Proc. Natl. Acad. Sci. U.S.A. 67:1715–1721.

———. 1975. Assembly of species communities. Pp. 342–444 *in* Ecology and evolution of communities (M. L. Cody and J. M. Diamond, eds.). Belknap, Cambridge, Massachusetts.

Emlen, J. M. 1973. Ecology: an evolutionary approach. Addison-Wesley Publishing Co., Reading, Massachusetts.

Godfrey, W. E. 1966. The birds of Canada. Natl. Mus. Canada Bull. 203. Ottawa, Ontario.

Grant, P. R. 1966a. Ecological compatibility of bird species on islands. Am. Nat. 100:451–462.

———. 1966b. The density of land birds on the Tres Marias Islands in Mexico. I. Numbers and biomass. Can. J. Zool. 44:391–400.

Klopfer, P. H. and R. H. MacArthur. 1960. Niche size and faunal diversity. Am. Nat. 94:293–300.

——— and ———. 1961. On the causes of tropical species diversity: niche overlap. Am. Nat. 95:223–226.

Lynch, J. F. and N. K. Johnson. 1974. Turnover and equilibria in insular avifaunas, with special reference to the California Channel Islands. Condor 76:370–384.

MacArthur, R. H. and E. O. Wilson. 1963. An equilibrium theory of insular zoogeography. Evolution 17:373–387.

——— and ———. 1967. The theory of island biogeography. Monogr. Pop. Biol. 1. Princeton University Press. Princeton, N.J.

———, J. H. Diamond and J. R. Karr. 1972. Density compensation in island faunas. Ecology 53:330–342.

———, J. MacArthur, D. MacArthur and A. MacArthur. 1973. The effect of island area on population densities. Ecology 54:657–658.

Morse, D. H. 1971. The foraging of warblers isolated on small islands. Ecology 52:216–228.

———. 1977. The occupation of small islands by passerine birds. Condor 79:399–412.

Peters, H. S. and T. D. Burleigh. 1951. The birds of Newfoundland. Nfld. Dept. Nat. Resour., St. John's, Newfoundland.

Pielou, E. C. 1966a. Shannon's formula as a measure of species diversity: its use and misuse. Am. Nat. 100:463–465.

———. 1966b. The measure of diversity in different types of biological collections. J. Theoret. Biol. 13:131–144.

Power, D. M. 1976. Avifauna richness on the California Channel Islands. Condor 78:394–398.

Rotenberry, J. T. 1978. Components of avian diversity along a multifactorial climatic gradient. Ecology 59:693–699.

Rowe, J. S. 1972. Forest regions of Canada. Dept. Environ. Can. For. Serv. Publ. No. 1300. Information Canada, Ottawa, Ontario.

Simberloff, D. S. and E. O. Wilson. 1969. Experimental zoogeography of islands: the colonization of empty islands. Ecology 50:278–295.

Sokal, R. R. and F. J. Rohlf. 1969. Biometry. W. H. Freeman, San Francisco, California.

Terborgh, J. and J. Faaborg. 1973. Turnover and ecological release in the avifauna of Mona Island, Puerto Rico. Auk 90:759–779.

———, ——— and H. J. Brockman. 1978. Island colonization by Lesser Antillean birds. Auk 95:59–72.

Vassallo, M. I. and J. C. Rice. Ecological release and ecological flexibility in habitat use and foraging behavior of an insular avifauna. Wilson Bull. In press.

Yeaton, R. I. and M. L. Cody. 1974. Competitive release in island Song Sparrow populations. Theoret. Pop. Biol. 5:42–58.

DEPT. BIOLOGY, MEMORIAL UNIV. OF NEWFOUNDLAND, ST. JOHN'S, NEWFOUNDLAND A1B 2X8 CANADA. (PRESENT ADDRESS JCR: CENTER FOR ENVIRONMENTAL STUDIES, ARIZONA STATE UNIV., TEMPE, ARIZONA 85281.) ACCEPTED 1 OCT. 1980.

INTERNATIONAL COMMISSION ON ZOOLOGICAL NOMENCLATURE

The following opinion has been published by the ICZN in the Bulletin of Zoological Nomenclature, Vol. 38, Pt. 2, 30 Apr. 1981: Opinion No. 1180 (p. 12) "*Thamnophilus amazonicus* Sclater, 1858 (Aves): conserved." The ICZN cannot supply separates of Opinions.

Wilson Bull., 93(3), 1981, pp. 350–356

ENVIRONMENTAL INFLUENCE ON SOARING IN WINTERING RED-TAILED HAWKS

Charles R. Preston

A variety of environmental factors are known to influence the flight activity of diurnal raptors. Craighead and Craighead (1956) reported that flight by wintering Red-tailed Hawks (*Buteo jamaicensis*) decreased markedly during periods of "bad weather." Schnell (1967) demonstrated that Rough-legged Hawks (*B. lagopus*) flew significantly less as wind velocity, barometric pressure and ambient temperature decreased, and as cloudiness and relative humidity increased. Similarly, Bildstein (1978) reported that variations in solar radiation, ambient temperature, wind velocity, relative humidity and precipitation were accompanied by shifts in the flight activity of 4 species of open habitat raptors. In one of the few quantitative studies dealing exclusively with soaring flight, Henty (1977) showed that soaring activity in several raptor species increased as ambient temperatures increased.

In this study, I used multivariate statistical techniques to investigate the effects of several environmental factors on the soaring activity of wintering Red-tailed Hawks in northwestern Arkansas. I also examined the influence of environmental factors on habitat use and altitude of soaring hawks.

STUDY AREA AND METHODS

The study was conducted in a 244-km^2 area near Centerton, Benton Co., Arkansas. There the flat to gently rolling terrain comprised scattered patches of pastureland, mixed hardwoods, old fields and cultivated fields. The few distinct ridges in the study area were grown primarily in mixed hardwoods. Woodlots and pastures together comprised about 85% of the study area.

Data were collected on 12 days (6 h/day) between 14 December 1976 and 25 February 1977 and between 1 December 1977 and 28 January 1978. I located hawks by driving along secondary roads throughout the study area and did not knowingly collect data on any individual hawk more than once in a day. I measured ambient temperature and relative humidity every hour afield with a sling psychrometer. All other weather data were recorded as each hawk was observed. A Dwyer wind meter was used to measure wind velocity at chest height. Solar illumination was measured with an illuminometer. Percent cloud cover was obtained with a circular mirror, 15 cm in diameter, marked with a 25-unit grid. This technique is described in detail elsewhere (Preston 1980).

In addition to weather variables, measures of habitat use were obtained for 50 soaring hawks chosen at random. Due to time restrictions, it was not feasible to sample the habitat below every soaring hawk observed. The site above which a hawk was soaring when first observed was considered the center of a circular 0.162-ha sampling area. Four orthogonal

Table 1
Mean, Standard Deviation and Range of Each Weather Parameter

	$\bar{x} \pm$ SD	Range
Ambient temp. (°C)	2.8 ± 7.31	−16.0–14.0
% relative humidity	49.5 ± 12.34	21.0–79.0
Wind velocity (mph)	10.1 ± 9.77	0.0–31.0
Solar illumination (foot candles)	702.0 ± 378.25	105.0–1800.0
% cloud cover	42.8 ± 30.96	0.0–100.0

transects were established from the center of each area, the first being set by the random position of the crosshairs of a sighting tube. Each transect was 45 m long and constituted the radius of the 0.162-ha circle. The habitat type (pasture, old field, cropland, woodlot) encountered at each of 25 random stops along each transect was recorded. These 100 stops were used to calculate habitat percentages for each sampling area. The technique is modified from James and Shugart (1970).

The soaring altitude of each of these 50 hawks was estimated using a transparent pane of glass marked with silhouette representations of Red-tailed Hawks as they would appear at various distances, up to 92 m from the observer. A taxidermy specimen was used to calibrate the scale. Only 3 of the 50 hawks were observed soaring above 92 m. Estimates derived from the scale are subject to some error due to the intraspecific size variation.

The data were analyzed using statistical programs in the computer library at the University of Arkansas. The 72 h of data were separated initially into 24 three-h observation periods (2/observation day) and the mean value of each weather variable was calculated for each observation period. The percentage of hawks soaring when first observed was also calculated for each observation period. Pearson's product-moment correlation analysis (Sokal and Rohlf 1969) was used to test for associations between environmental factors and soaring activity and habitat use. After transforming the data to minimize non-normality and heteroscedacticity (Box and Cox 1964, Sokal and Rohlf 1969, Andrews et al. 1971), a multivariate analysis of variance (MANOVA) (Morrison 1967) with a step-down procedure (Bargmann 1962) was used to test for a significant difference in soaring incidence with respect to environmental factors. Then discriminant function scores were generated and were used to characterize environmental conditions associated with soaring activity.

RESULTS AND DISCUSSION

The means and standard deviations of each weather factor are given in Table 1. Table 2 shows that the percentage of hawks observed soaring increased significantly as relative humidity and cloud cover decreased, and as wind velocity and solar illumination increased. Because these 4 variables were highly intercorrelated, partial correlation analysis (Morrison 1967) was used to clarify the association between each of these factors and the incidence of soaring. The partial correlation coefficients (wind velocity 0.907; $P < 0.001$, illumination 0.101; $P > 0.05$, cloud cover −0.103; $P > 0.05$, relative humidity −0.036; $P > 0.05$) show that only

Table 2

Product-Moment Correlation Coefficients for Environmental Factors and the Incidence of Soaring During Observation Periods[a]

	Ambient temp.	Relative humidity	Wind velocity	Solar illumination	% cloud cover
% of hawks soaring	0.223	−0.729*	0.864*	0.799*	−0.765*
Ambient temperature		0.211	0.209	0.207	0.158
Relative humidity			−0.707*	−0.764*	0.758*
Wind velocity				0.701	−0.768*
Solar illumination					−0.871*

[a] Twenty-four 3-h observation periods.
* Indicates significant correlation at $P \leq 0.05$.

wind velocity was associated significantly with the incidence of soaring when other variables were held constant. Fig. 1 illustrates the observed relationship between wind velocity and incidence of soaring.

Similarly, MANOVA showed a highly significant difference in soaring activity with respect to environmental variables ($-m \ln \lambda = 76.40$, $P < 0.001$). The associated step-down procedure identified wind velocity as the only variable which, taken by itself, contributed significantly ($P < 0.001$) to the difference. The discriminant function (a linear function of the original environmental variables) stressed those factors separating soaring from non-soaring activity (Sokal and Rohlf 1969). Wind velocity, illumination, cloud cover and relative humidity were highly correlated with the discriminant function (Table 3) and thus were important in characterizing a weather gradient associated with soaring activity (Fig. 2).

In his discussion of soaring, Cone (1962) differentiated static soaring involving the use of rising air columns, from dynamic soaring involving the use of wind gradients. He further classified static soaring into declivity (or slope) and thermal soaring. Declivity currents arise when wind is de-

Table 3

Coefficients of Correlation Between Each Weather Parameter and Discriminant Function (After Data Stabilization)

	Discriminant function
Ambient temperature	0.148
Relative humidity	−0.459
Wind velocity	0.901
Solar illumination	0.595
Cloud cover	−0.503

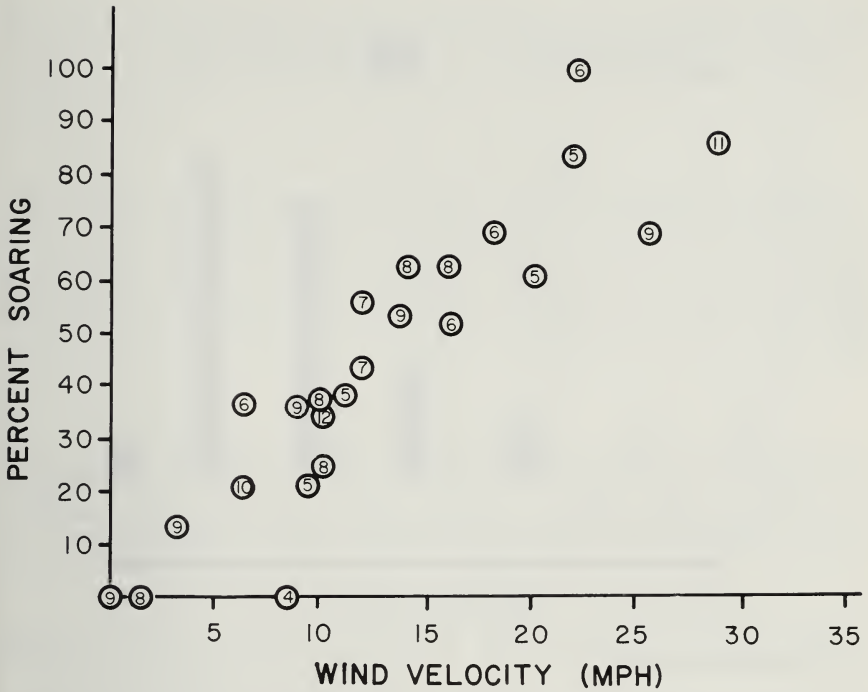


FIG. 1. Observed association between wind velocity and the incidence of soaring for each of the 24 three-h observation periods. Circled numbers indicate how many hawks were observed during each period.

flected upward by surface obstacles such as hills. Thermals are formed as surface layers of air become warmed and/or moisture-laden by the sun-heated earth. These less dense bubbles of warm air rise steadily. Cone (1962) concluded that thermal soaring was the most important method of soaring flight used by land birds. However, Pennycuick (1972) emphasized that among raptors the use of declivity currents for soaring above hillsides is very common.

The association that I found between wind velocity and soaring activity could indicate use of either declivity or dynamic soaring. Although the relatively low-aspect-ratio wings of Red-tailed Hawks are not particularly well-adapted for any method of soaring, they are common in birds specializing in static soaring (Cone 1962, Welty 1962, Pennycuick 1972). Furthermore, dynamic soaring has generally not been considered important to land soarers mainly due to the lack of a wind gradient above land masses (Pennycuick 1972). Correlation analysis showed general independence between environmental factors and habitat use. However, there was a sig-

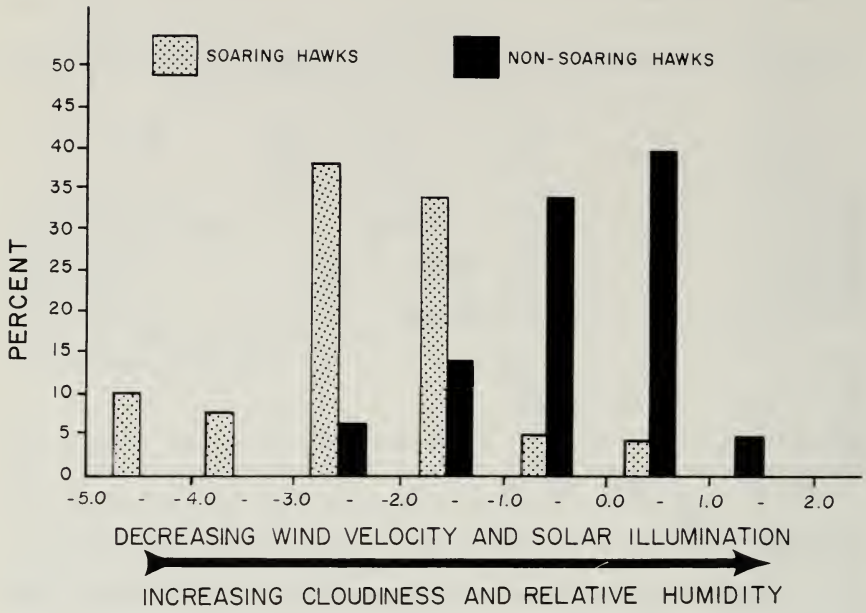


FIG. 2. Separation between soaring (N = 77) and non-soaring (N = 103) hawks along the discriminant function axis.

nificant positive correlation between wind velocity and soaring altitude ($P < 0.05$). Higher wind velocities can increase the declivity "soaring zone" surrounding hills and ridges, thus allowing the hawks to soar higher (Pennycuick 1972, Grace 1977). The relationship between wind velocity and soaring activity needs to be quantified in relatively barren, flat areas devoid of significant declivity currents. Reports by Hankin (1913), Cone (1962) and Henty (1977) indicate that increasing ambient temperature, rather than wind velocity, may be the dominant weather factor associated with soaring activity in the tropics and during temperate seasons when conditions are conducive to thermal soaring. Because adverse conditions such as fog or precipitation depress most raptor flight activity (Craighead and Craighead 1956, Schnell 1967, Bildstein 1978), it would be an oversimplification to attribute absolute control of soaring frequency to 1 environmental factor in any season or climate.

Although early reports emphasized hunting as the primary function of *Buteo* soaring, Wakeley (1978) found that Ferruginous Hawks (*B. regalis*) spent far more time soaring than predicted from capture/cost ratios for that hunting method. Thermoregulation, territorial display and exploration have been mentioned as some alternative functions of soaring (see Wake-

ley 1978). Studies designed to determine *Buteo* species distributions with respect to both thermal and declivity soaring opportunities will prove useful in evaluating the importance of soaring (other than migratory) as an adaptive activity.

SUMMARY

The incidence of soaring by Red-tailed Hawks wintering in northwestern Arkansas fluctuated with several weather parameters. The percentage of hawks observed soaring increased as wind velocity and solar illumination increased, and as cloud cover and relative humidity decreased. Wind velocity was the most important factor associated with soaring incidence. Hawks also soared at greater altitudes as wind velocity increased. The results are interpreted to reflect the use of declivity updrafts to soar under conditions not conducive to thermal soaring.

ACKNOWLEDGMENTS

I wish to thank D. A. James for advice and encouragement during the study. P. S. Hatcher provided valuable assistance with some of the fieldwork. I am also indebted to J. Ballam, G. D. Schnell and K. L. Bildstein for comments on various versions of the manuscript. The study was supported in part by the Arkansas Audubon Society Trust Fund and the Department of Zoology, University of Arkansas, Fayetteville, Arkansas.

LITERATURE CITED

Andrews, D. F. R., R. Gnanidesikan and J. F. Warner. 1971. Transformation of multivariate data. Biometrics 27:825–840.

Bargmann, R. 1962. Representative ordering and selection of variables. Coop. Res. Proj. No. 1132, Final Rept. U.S. Off. Health, Educ., Welfare, Washington, D.C.

Bildstein, K. L. 1978. Behavioral ecology of Red-tailed Hawks (*Buteo jamaicensis*), Rough-legged Hawks (*B. lagopus*), Northern Harriers (*Circus cyaneus*), American Kestrels (*Falco sparvarius*), and other raptorial birds wintering in south-central Ohio. Ph.D. diss., Ohio State Univ., Columbus, Ohio.

Box, G. E. P. and D. R. Cox. 1964. An analysis of transformations. J. Roy. Stat. Soc. 26:211–252.

Cone, C. D. 1962. Thermal soaring of birds. Am. Sci. 50:180–209.

Craighead, J. J. and F. C. Craighead, Jr. 1956. Hawks, owls, and wildlife. Stackpole Co., Harrisburg, Pennsylvania.

Grace, J. 1977. Plant response to wind. Academic Press, New York, New York.

Hankin, E. H. 1913. Animal flight. Watts and Co., London, England.

Henty, C. J. 1977. Thermal soaring of raptors. Br. Birds 70:471–475.

James, F. C. and H. H. Shugart, Jr. 1970. A quantitative method of habitat description. Audubon Field Notes 24:727–738.

Morrison, D. F. 1967. Multivariate statistical methods. McGraw Hill, New York, New York.

Pennycuick, C. J. 1972. Animal flight. Edward Arnold, London, England.

Preston, C. R. 1980. Differential perch-site selection by color morphs of the Red-tailed Hawk (*Buteo jamaicensis*). Auk 97:782–789.

Schnell, G. D. 1967. Environmental influence on the incidence of flight in the Rough-legged Hawk. Auk 84:173–182.

Sokal, R. R. and F. J. Rohlf. 1969. Biometry. W. H. Freeman, San Francisco, California.
Wakeley, J. S. 1978. Hunting methods and factors affecting their use by Ferruginous Hawks. Condor 80:327–333.
Welty, J. C. 1962. The life of birds. W. B. Saunders Co., Philadelphia, Pennsylvania.

DEPT. ZOOLOGY, UNIV. ARKANSAS, FAYETTEVILLE, ARKANSAS 72701. ACCEPTED 20 OCT. 1980.

THE WILSON ORNITHOLOGICAL SOCIETY ANNOUNCES AWARDS

Louis Agassiz Fuertes, Margaret Morse Nice and Paul A. Stewart Awards

Fuertes Awards are available to all ornithologists although graduate students and young professionals are preferred. Nice Awards are intended for independent researchers without access to funds and facilities available at colleges and universities and thus are restricted to amateurs, including high school students. Any type of research may be funded by both Fuertes and Nice awards.

Stewart Awards are available to any applicant for ornithological research, especially studies of bird movements based on banding and analysis of recoveries and returns and investigations in economic ornithology.

One Fuertes Award of at least $100.00, one Nice Award of $100.00 and one or more Stewart Awards of $200.00 each will be made. Interested applicants should write to Carl D. Marti, Department of Zoology, Weber State College, Ogden, Utah 84408. Completed applications must be received by 1 March 1982. Decisions will be announced at the 1982 Annual Meeting of the Wilson Ornithological Society to be held 6–9 May 1982.

Aaron M. Bagg Student Membership Awards

Student membership awards in The Wilson Ornithological Society providing a 1-year membership in the Society are available for persons not currently members of the Society. These awards are funded by a donation made in the memory of Aaron M. Bagg, a former president of the Society. Application forms for 1982 awards may be obtained from John L. Zimmerman, Division of Biology, Kansas State University, Manhattan, Kansas 66506. Deadline for applying is 1 November 1981.

Wilson Bull., 93(3), 1981, pp. 357–362

BREEDING SUCCESS IN AN ISOLATED POPULATION OF ROCK DOVES

David E. Preble and Frank H. Heppner

There has been considerable discussion about actual or potential means by which some animal populations might maintain stability in the face of variable environmental pressures. This paper reports the results of a 2-year study of breeding success in an isolated population of Rock Doves (*Columba livia*, hereafter referred to as the pigeon) which suggests that an increase in egg predation is followed by a lowering of the adult nest desertion rate, thus maintaining the recruitment of new individuals into the population at a constant rate.

STUDY AREA AND METHODS

The study involved a breeding colony of 45–55 pigeons (depending on season) in the abandoned Plum Beach lighthouse in Narragansett Bay, Rhode Island. This structure is separated from land 0.8 km to the west and 1.2 km to the east. Food is readily available year around near habitation to the west and east from bird feeders and natural sources, but there is no food or water on the lighthouse itself. Severe storms and fog during the winter could cut off access to food and affect adult mortality. Great Cormorants (*Phalacrocorax carbo*) roosted on the upper outside portion of the structure. The Black-crowned Night Heron (*Nycticorax nycticorax*) was an occasional summertime visitor. No other vertebrates were known to be in the lighthouse. To minimize disturbance, we did not band individuals, and so do not have an accurate measure of the number of non-breeders or colony size. The number of active nests ranged from two during breeding lows to 25 at breeding peaks.

To determine the recruitment rate (total breeding success, or number of young fledged per eggs laid), we visited the lighthouse every 1–2 weeks in 1971 and 1972. On each visit, the location of every nest, egg and young was recorded on maps of each of the 5 levels of the 8-m-diameter lighthouse. The nests were scattered through each level, and were no closer than 1 m to each other. During the first full year of observation we left the nests untouched and in the second year we removed a fraction of eggs laid, simulating the action of an egg predator. The objective was to see if egg desertion would drop by an amount corresponding to the number removed, thus maintaining a constant recruitment rate. This artificial predation was performed by counting the number of eggs laid since the last visit. Twenty percent of this number were then removed from the total number present.

The removed eggs were checked for fertility and stage of development. Egg replacement by the birds would have biased the results, but the pigeon is a determinate layer with a 2-egg clutch-size (Sturkie 1954). At the end of another full year, the results were tabulated and compared both with the data from the first year, and with breeding data from Murton and Clarke (1968).

RESULTS

Breeding season.—The Plum Beach light pigeons are year-round breeders, but demonstrate a different annual pattern than seen in the British

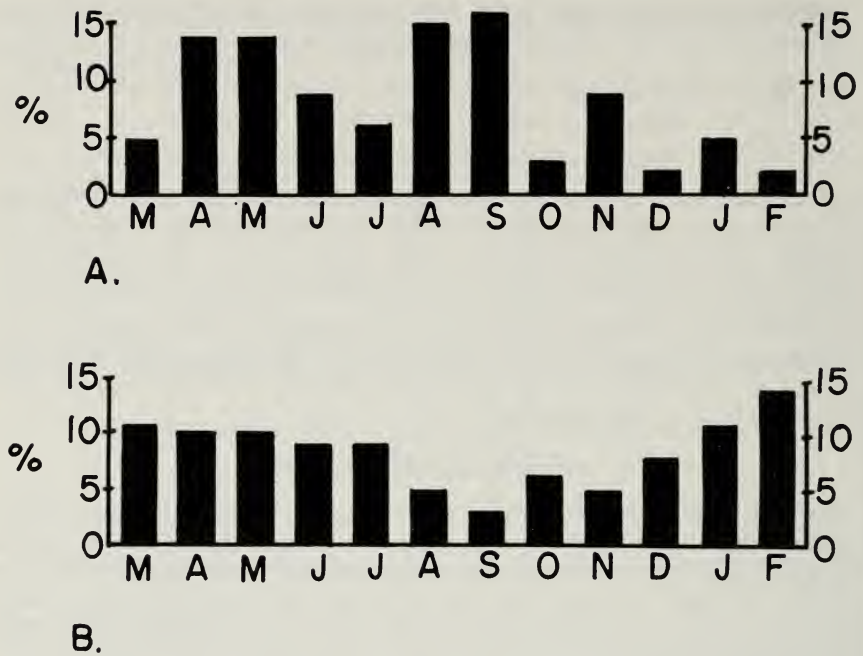


FIG. 1. Number of eggs (expressed as a monthly percent of the year's total) laid in each month by pigeons (A) in Yorkshire, England (Murton and Clarke 1968); composite of 2 years, 1965–66; (B) in Narragansett Bay, Rhode Island; monthly average for the years 1971–72 and 1972–73.

Isles (Fig. 1) by Murton and Clarke (1968) or Lees (1946). Lees found a constant low level of breeding in northern Scotland, with high activity at 4 periods; April, August, November and January. Murton and Clarke (1968) found the same pattern in England, with the spring and summer periods accounting for 60% of the total annual breeding. At the Plum Beach light, however, there was a marked low in August and September, followed by a rather steady rise to a high point in February and March, which was then followed by a steady drop through the spring until the August low point was reached again.

Breeding success.—The observations recorded at each visit to the lighthouse are shown in Table 1. The difference between the years in total egg and total juvenile observations is the result of more visits in the second year, since the total egg and juvenile observation figures are the sum of the total number of eggs or juveniles present at each visit. The total number of new eggs and total number of new juveniles was unaffected by the number and frequency of visits, since visits were close enough together

Table 1

Comparison of Breeding Success of Pigeons in Non-isolated (Murton and Clarke 1968) and Isolated (Preble 1973) Lighthouses

	Murton and Clarke		Preble	
	1965	1966	1971–72	1972–73
Total egg observations	—	—	948	1295
Total juvenile observations	—	—	547	860
Total eggs laid	346	409	562	672
Total no. hatched	211	286	312	388
% hatched	61	70	56	58
% egg predation	25	15	1 (8)[a]	22 (145)
% infertile	5	5	5[b]	4 (6)
% deserted	9	10	38 (218)	16 (106)
% fledged of eggs hatched	70	71	77[c]	83[c]
% fledged of eggs laid	43	49	42[c]	48[c]

[a] Numbers in parentheses are actual numbers of eggs.
[b] Approximation, see text.
[c] Calculated value, see text.

that no eggs could be laid or juveniles hatched between visits without being counted. The lower new egg and new juvenile production for the first year is, in part, due to the termination of the first year's data acquisition, due to adverse weather, 1 full week before the end of a complete year, in February 1972. Inflating the production of the second year was the high number of eggs laid in January and February 1973, probably due to an unusually mild and snowless winter which resulted in a large number of adults in breeding condition.

The parameters involved in breeding success for the 2 years at Plum Beach light and, for comparison, the 2 years that Murton and Clarke (1968) worked on the beacon tower at Flamborough Head, are also shown in Table 1. On the Plum Beach light, 1971–72, total egg predation consisted of 8 eggs (1%) pecked open or removed between 10 June and 3 August 1971. During 1972–73 natural predation consisted of 9 eggs pecked open or removed, and was supplemented by the experimental removal of an additional 136 eggs to bring the total "predation" level for that year to 22%.

The number of infertile eggs (Table 1) was determined in 1972–73 by opening and examining the eggs removed. The number of infertile eggs was six, which is 4.4% of the total, or 1.8–9.4% at 95% confidence limits. This value is in the same range ($\chi^2_{(2)} = 0.01$, $P > 0.99$, NS) as the 5% (3.6–6.8% at 95% confidence limits) reported by Murton and Clarke (1968). Since there was no nest disturbance in 1971–72, it was impossible to check

directly for infertility by opening and examining the eggs, although it was indirectly determined that there was little or no change in egg fertility between the years of the study (Preble 1973). Since there was a constant level of infertility in the 2 years, and there was no significant difference in fertility between the British and American populations, Murton and Clarke's (1968) 5% figure is used in all calculations (Table 1).

Egg desertion (Table 1) was determined on the assumption that a fertile egg which is not destroyed by predation will hatch if incubated. Failure to incubate then constitutes desertion of the egg. Desertion may be caused by adult mortality or abandonment. We determined the number deserted by subtracting the number removed by predation and infertility from the number that failed to hatch. In 1971–72, desertion accounted for 38% of the total number of eggs laid, while in 1972–73 it accounted for 16%.

The young fledged per young hatched (juvenile success) and the young fledged per eggs laid (total success, Table 1), were determined indirectly. If there was no mortality at any state of the reproductive cycle, then we expected that a ratio of the total number of eggs present and juveniles present on each visit would equal the ratio of the amount of time an individual spent in the egg compared to the amount of time spent as a juvenile: 17.5 and 24 days, respectively (Whitman 1919, Goodwin 1967, Murton and Clarke 1968). Taking the total number of egg observations for 1971–72, and the known time individuals spent in the egg as a juvenile, and assuming no mortality of eggs or juveniles, the expected number of observations of juveniles would reflect the following ratio: 17.5 days/24 days = 948 egg observations/X. The expected number of observations of juveniles assuming neither egg nor juvenile mortality (X) then equals 1300. The juvenile mortality was determined as follows. Since the number hatched (Table 1) shows that the actual egg survival was 56% (egg mortality 44%), then the expected number of observations of juveniles if there had been no juvenile mortality, but with the observed egg mortality is: $0.56 \times 1300 = 728$ = expected number of observations of juveniles with the observed egg mortality. Since there were only 547 actual observations of juveniles (Table 1) then the level of juvenile success must be: 547 actual observations/728 expected observations = 75% fledged of eggs hatched, or a juvenile mortality of 25% of the eggs hatched. Since 312 eggs hatched (Table 1), and inferentially 75% were successfully fledged, then the number that fledged of all the eggs laid equals: $0.75 \times 312 = 234$ eggs fledged of 562 eggs laid. The total success (fraction of eggs laid) then becomes: 234 eggs fledged/562 eggs laid—42%. The same procedure applied to the data from 1972–73 yields a fraction fledged of eggs hatched of 83% and a fraction fledged of eggs laid of 48%.

It thus appears that net recruitment, measured by total nest success,

remained at approximately the same level (42% in 1971–72, and 48% in 1972–73; $t_s = 1.29$, $P < 0.90$) although egg "predation" significantly differed, from 1% in the first year to 21% in the second year ($t_s = 8.03$, $P > 0.001$). The fraction fledged of eggs hatched (Table 1) is somewhat higher at Plum Beach light than in England, and somewhat higher at Plum Beach light in 1972–73 than in 1971–72, probably reflecting the milder winter.

DISCUSSION

Population homeostasis in the pigeon could be maintained through a mechanism which regulates the recruitment rate of young adults by means of a variable rate of egg desertion. Lack (1966, 1968) suggested that each species produces as many young as it can successfully rear in a food-limited environment and that adult mortality through starvation is the variable factor that controls population size. Skutch (1967) has argued that some species could produce more young than they do, and that the rate of egg-laying may be a factor. Fretwell (1969) has attempted to mediate this dispute by suggesting that there may be a dominance hierarchy which extends to nestlings, the lower ones being most subject to selective mortality in hard times.

In prior work on the breeding biology of the pigeon, egg predation was sufficiently high to mask the effects of egg desertion (Murton and Clarke 1968). On the Plum Beach lighthouse, where the rate of natural egg predation is very low and suitable nest-sites are readily available, the results of this study suggest that the population has a breeding reserve which enables it to remain stable through selective desertion of eggs. Although there is insufficient evidence to do more than speculate, this desertion appears to be a behavioral mechanism, rather than the result of starvation of adults. If the latter was the case, then one would expect to see a high rate of desertion of juveniles as well as eggs. The desertion, however, is suffered primarily by eggs, and only when predation of eggs is low.

There are several mechanisms that might account for this differential desertion. Wynne-Edwards' (1963) model of group selection is not incompatible with the observations reported here, but the more recent concept of kin selection (Eberhard 1975) requires fewer assumptions about conditions existing in the colony. The observations here do support the idea of population regulation based on behavior, but cannot help to differentiate between the competing models of behavioral regulation.

SUMMARY

Breeding success (number fledged/eggs laid) and nest desertion were determined in a flock of Rock Doves (*Columba livia*) breeding in an isolated, abandoned lighthouse in Narragansett

Bay, Rhode Island, over a 1-year period. Breeding success was 42% in that year and 38% of nests with eggs were deserted. In the following year, 20% of eggs laid were removed. Nest desertion dropped to 16%, while breeding success was 48%, suggesting that recruitment might be related to nest desertion.

ACKNOWLEDGMENTS

Our thanks to the Rhode Island Department of Natural Resources for permission to visit the lighthouse, and C. Robert Shoop for critically reading the manuscript.

LITERATURE CITED

Eberhard, M. J. W. 1975. The evolution of social behavior by kin selection. Quart. Rev. Biol. 50:1–33.

Fretwell, S. D. 1969. The adjustment of birth rate to mortality in birds. Ibis 111:624–627.

Goodwin, D. 1967. Pigeons and doves of the world. British Museum (Nat. Hist.), London, England.

Lack, D. 1966. Population studies of birds. Clarendon Press, Oxford, England.

———. 1968. Ecological adaptations for breeding in birds. Methuen and Co., London, England.

Lees, J. R. 1946. All the year breeding of the Rock Dove. Br. Birds 39:136–141.

Murton, R. K. and S. P. Clarke. 1968. Breeding biology of Rock Doves. Br. Birds 61:429–448.

Preble, D. E. 1973. Breeding homeostasis in the feral Rock Dove (*Columba livia*). M.S. thesis, Univ. Rhode Island, Kingston, Rhode Island.

Skutch, A. F. 1967. Adaptive limitation of the reproductive rate of birds. Ibis 109:579–599.

Sturkie, P. D. 1954. Avian physiology. Comstock Publishing Assoc., Ithaca, New York.

Whitman, C. O. 1919. Posthumous works, Vol. 3. The behavior of pigeons (H. A. Carr, ed.). Carnegie Inst., Publ. 257. Washington, D.C.

Wynne-Edwards, V. C. 1963. Intergroup selection in the evolution of social systems. Nature 200:623–626.

DEPT. ZOOLOGY, UNIV. RHODE ISLAND, KINGSTON, RHODE ISLAND 02881. ACCEPTED 22 OCT. 1980.

Wilson Bull., 93(3), 1981, pp. 363–371

RELATIVE ABUNDANCE OF GEORGIA CAPRIMULGIDS BASED ON CALL-COUNTS

Robert J. Cooper

In recent years there has been much interest in the southward range expansion of the Whip-poor-will (*Caprimulgis vociferus*). Baker and Peake (1966) made several listening counts for Whip-poor-wills and Chuck-will's-widows (*C. carolinensis*) around Athens, Georgia, and determined that the Whip-poor-will was extending its summer range southward to include the lower Piedmont of Georgia. Allen (1979) found the Whip-poor-will to be fairly abundant in the suburban areas of Clarke County although it was greatly outnumbered by the Chuck-will's-widow. He reported substantial clustering in the local distribution of the Whip-poor-will, so that in some places it had actually replaced the Chuck-will's-widow. Prior to this, the Whip-poor-will had been described as "an uncommon transient south of the mountain counties" (Burleigh 1958). Odum (1943) reported the Whip-poor-will as not having substantially changed its distribution in the previous 35 years. By 1968, however, the Whip-poor-will was listed as a locally common summer resident around Athens, Georgia (Tramer 1968). The Chuck-will's-widow has always been a common summer resident in this area.

Because caprimulgids are often heard but seldom seen, listening counts made at periodic intervals along secondary and dirt roads are a logical way to determine their abundance. Brauner (1952) related dawn and dusk activity of Poor-wills (*Phalaenoptilus nuttallii*) to light intensity, and related duration of the active period of this species to several factors, especially moon phase. Mengel and Jenkinson (1971) also mentioned the importance of moonlight relative to caprimulgid calling activity. Harper (1938) found that on moonless nights, Chuck-will's-widow's singing appeared to be limited to brief periods at dusk and daybreak. On moonlit evenings, however, the birds continued to sing indefinitely. Baker and Peake (1966) mentioned the negative effect of wind on calling. These and other studies, however, have varied in both techniques and results so that the information is of little comparative value (Dillenbeck 1967, Nunley 1960).

The purpose of this study was to determine the relative abundance of Chuck-will's-widows and Whip-poor-wills in Clarke County, Georgia, from a series of call counts, and to correlate different environmental factors with calling activity.

METHODS

Athens, a city of 50,000 people, is located in the geographic center of Clarke County, which is characterized by gently rolling hills of red clay subsoils, with an average elevation of 700 ft (228.5 m). During the last 50 years the county has experienced much urbanization with numerous suburban developments.

In the southeast portion of the county, 20 roadside listening counts were made by the author from 13 April–23 July 1975, along main, secondary and dirt roads. Twenty permanent stations were established at approximately 0.5 mile (0.8 km) intervals. Barnett Shoals Road, a main road in a partially suburban area, contained the first 7 stations. The next 7 stations were on Belmont Road, a paved road running through farm land largely maintained as improved pasture. The final 6 stations were along a dirt road extending into pine-hardwood forest. Thus, it was possible to categorize the counts by land use type: either suburban, pasture, or forest. The counts were started from alternate ends of the route each evening at sundown, unless birds started to call prior to sundown. No counts were made at dawn. The time spent at each station was standardized at 3 min, although it was sometimes necessary to spend slightly more time at a station where many birds were calling. At each station the number of Whip-poor-wills and Chuck-will's-widows was recorded, in addition to vigorousness of song. Every effort was made to avoid counting the same bird twice. Data for 2 counts that took place during moderate to heavy rain were not included in the statistical analysis. Weather data were obtained from records at the nearby Clarke County Airport.

The effects of 7 variables (calendar date, sine curve date, temperature, relative humidity, visibility, wind velocity and moon phase) upon the number of calling Chuck-will's-widows and Whip-poor-wills were tested using the SAS statistical package programs (Barr and Goodnight 1972). Correlation procedures were used for Chuck-will's-widows and Whip-poor-wills both individually and collectively. Moon phase was expressed as a value on a 180° sine curve using the formula:

$$\text{moon phase} = \sin\left[180°\left(\frac{\text{nights since last new moon}}{\text{total nights between new moons}}\right)\right]$$

On nights when the count took place before moonrise, moon phase was treated as a new moon, with a value of zero. Date was expressed as both calendar date and as a value on a 360° sine curve using the formula:

$$\text{date} = \sin\left[360°\left(\frac{\text{day in year}}{365}\right)\right]$$

where day 1 is the vernal equinox.

Differences between numbers of Chuck-will's-widows and Whip-poor-wills in each habitat type was tested using Student's *t*-test. Differences in numbers of the same species between different habitat types were tested using analysis of variance and least significant difference procedures (Steel and Torrie 1960).

On the night of 24–25 May, a full lunar eclipse occurred. On this night 3 counts were taken: one during the waning period, one during the period of total eclipse, and one during the waxing period.

RESULTS AND DISCUSSION

Of all variables tested, moonlight had the most striking effect on singing activity. Only phase of the moon and calendar date showed significant correlations with numbers of singing birds. Moon phase showed a partic-

TABLE 1

TABLE OF CORRELATION COEFFICIENTS FOR TESTED VARIABLES POSSIBLY AFFECTING CALLING OF WHIP-POOR-WILLS AND CHUCK-WILL'S-WIDOWS

Variables	Singing birds		
	Whip-poor-wills	Chuck-will's-widows	Both species
Calendar date	−0.3899	−0.1747	−0.2877
Sine curve date	0.1681	0.3616	0.2591
Temperature	0.0557	0.3246	0.1825
Relative humidity	−0.0126	0.2325	0.1031
Wind velocity	0.2229	−0.0264	0.1049
Visibility	−0.0241	−0.2469	−0.1292
Moon phase	0.6372*	0.3841	0.5167**

* Significant at $P = 0.01$ level.
** Significant at $P = 0.001$ level.

ularly strong relationship ($r = 0.52$, $P \leq 0.001$) with numbers of singing birds. R^2 values were acceptable. Table 1 shows correlation coefficients of tested variables for Chuck-will's-widows, Whip-poor-wills and total birds. Moon phase showed a significant correlation ($P \leq 0.01$) with total numbers of singing birds and with Whip-poor-wills, but not with Chuck-will's-widows.

Except for moonlit nights, singing usually was restricted to the period between sunset and darkness. Singing Chuck-will's-widows and Whip-poor-wills were recorded 2.23 times as often and 3.15 times as often, respectively, when the moon was greater than half full as opposed to less than half full. The greatest single total for an evening was on the moonlit night of 27 April, when 80 birds were recorded. Some of these, and some on earlier counts, may have been transients. The full moon in May yielded similar results, but by July the birds seemed to have ceased most of their singing. No counts were taken during the full moon in June. Total numbers of calling birds of both species are shown in Fig. 1. Two counts that were subsequently eliminated from statistical analysis were taken during moderate to heavy rain, during which neither species was heard. Chuck-will's-widows were heard, however, on the evening of 31 May, when the rain slowed to a drizzle. Periods of high humidity did not lessen singing activity in either species, and periods after rains were highly productive (the 27 April count of 80 birds took place after a heavy rain with a relative humidity of 90% that evening).

Differences in numbers between species in different habitat types were tested using Student's t-test ($P \leq 0.05$). The results, not shown, are summarized as follows: (1) No significant difference in numbers of Chuck-

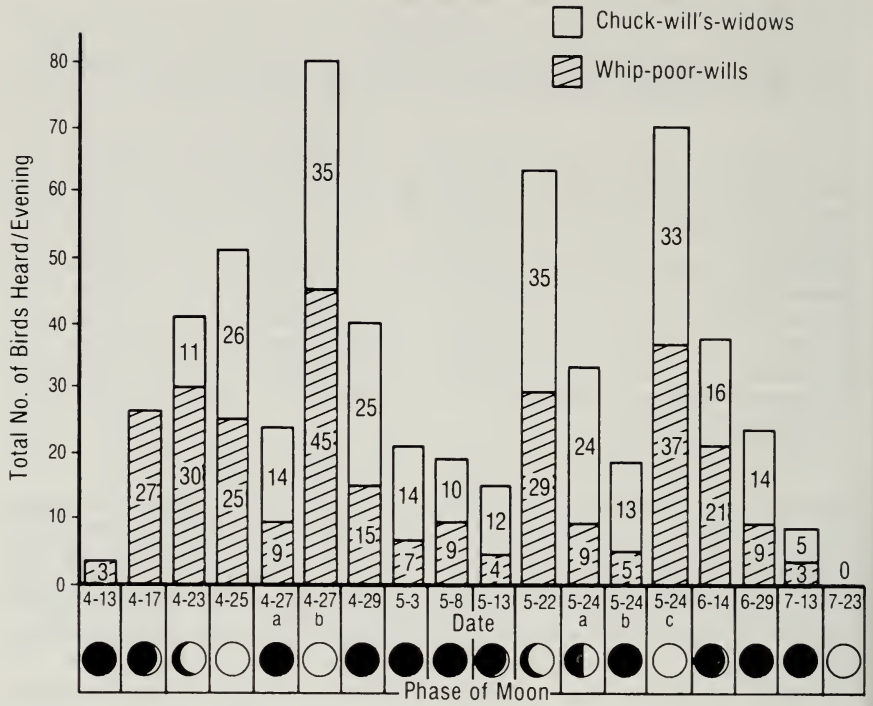


FIG. 1. Total numbers of birds recorded per count.

will's-widows and Whip-poor-wills was observed in the Barnett Shoals Road area. A total of 86 Chuck-will's-widows and 71 Whip-poor-wills was counted in this primarily suburban area. (2) A significant difference was observed between numbers of the 2 species in the Belmont Road area. The open habitat associated with pasture land was more favorable to Chuck-will's-widows. A total of 133 Chuck-will's-widows and 81 Whip-poor-wills was counted. (3) A significant difference was observed between numbers of the 2 species in the forested area in favor of Whip-poor-wills. A total of 70 Chuck-will's-widows and 129 Whip-poor-wills was counted.

Differences in numbers of the same species between habitat types were tested using analysis of variance and least significant difference procedures ($P \leq 0.05$). The results are summarized as follows:

(1) There was no significant difference between numbers of Chuck-will's-widows observed in the 3 habitat types.

(2) Whip-poor-wills were significantly more numerous in the forested area than in the other 2 habitat types. There was no significant difference between numbers of Whip-poor-wills observed in pasture and suburban areas.

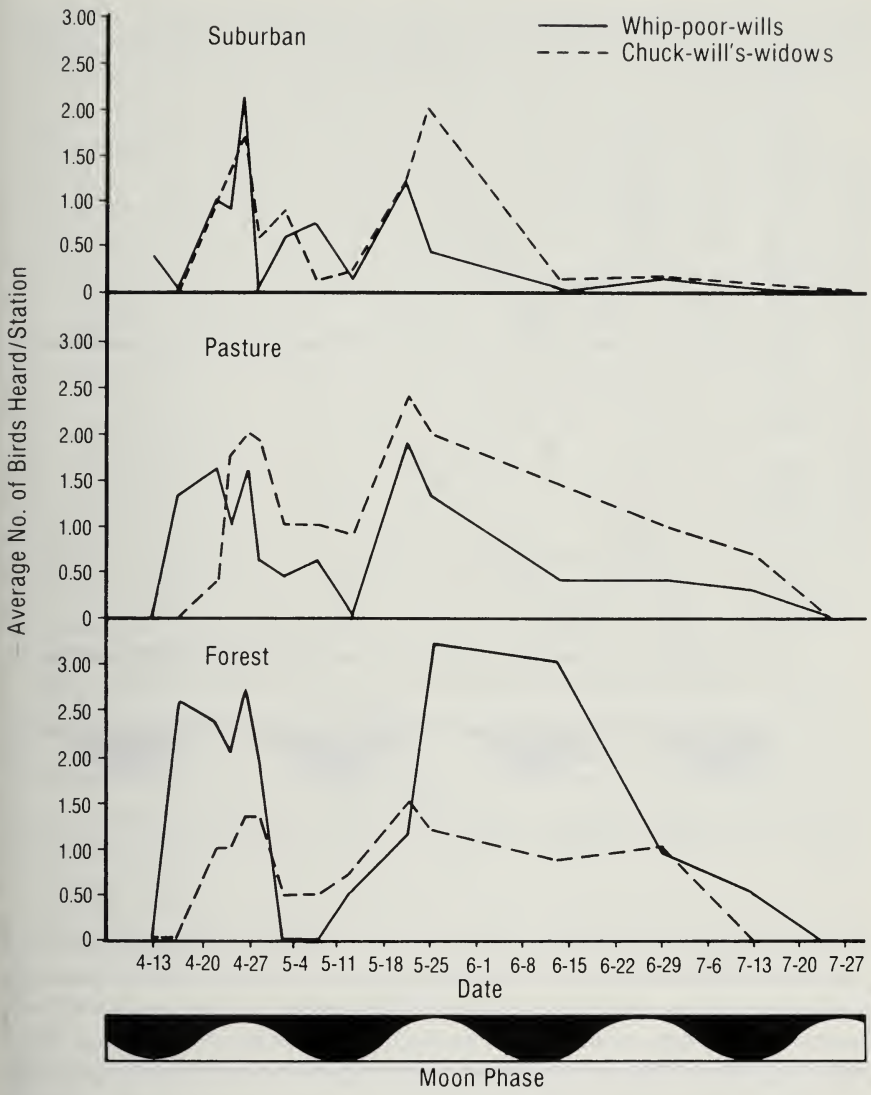


FIG. 2. The relative abundance of Whip-poor-wills and Chuck-will's-widows in suburban, pasture and forested areas.

Fig. 2 compares numbers of Chuck-will's-widows and Whip-poor-wills in each habitat type. Fig. 3 compares numbers of 1 species in the 3 habitat types. Each set of graphs shows 2 peaks occurring at the full moon in April and May.

The literature concerning habitat preferences of Whip-poor-wills and

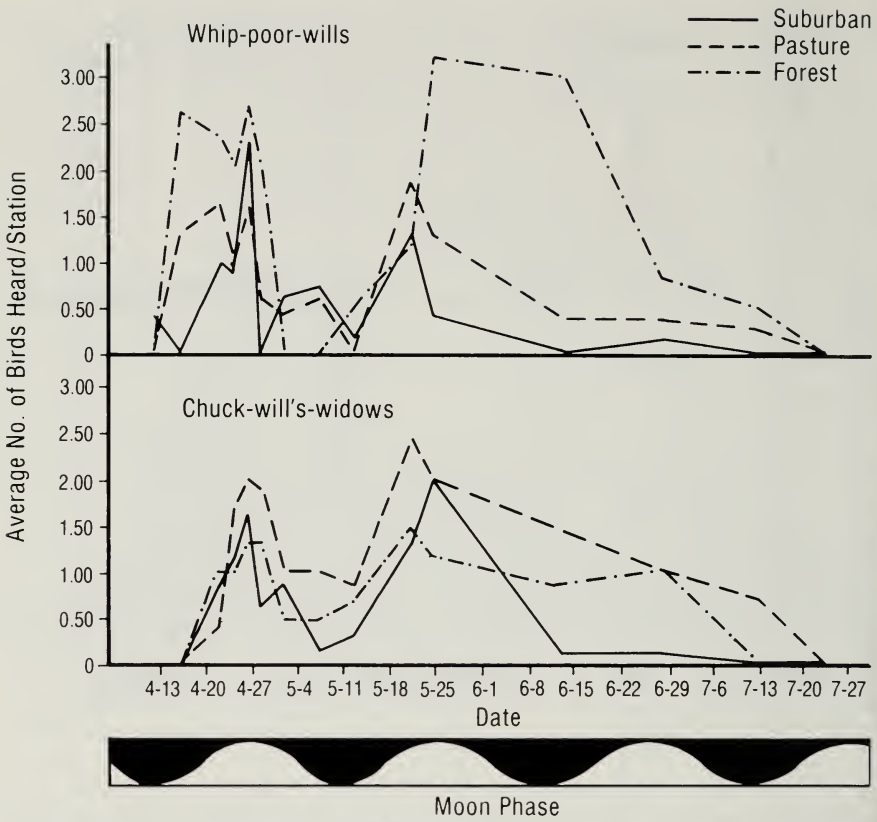


FIG. 3. The relative abundance of Whip-poor-wills and Chuck-will's-widows in 3 habitat types.

Chuck-will's-widows is inconsistent. In this study Chuck-will's-widows showed a relative affinity for open habitat and Whip-poor-wills showed a preference for wooded habitat. Bent (1940) reported Chuck-will's-widows active on the edges of woodlands bordering open field, often making sallies over the latter. Harper (1938) found that Chuck-will's-widows in the Okefenokee region preferred hammocks for roosting and more open country for feeding. Imhof (1976) reported both species occurring in woodlands of oak and pine. The Whip-poor-will was considered by Bent to be a woodland species that used small open areas for feeding. Allen (1979) found Whip-poor-wills in the Athens area to be restricted to a few areas, suburban in nature, characterized by a mixture of pasture and pine woods, with hardwoods restricted to creek bottoms. Baker and Peake (1966) found that the Whip-poor-will seemed limited to higher ground. Allen (1979)

could not confirm or refute this observation. In this study Whip-poor-wills were most abundant in the areas with the lowest elevation (<600 ft [182.8 m]), so that elevation can probably be eliminated as a limiting factor in range expansion of this species.

The southward range expansion of the Whip-poor-will appears to be related to a general southward invasion of northern species as discussed by Odum and Burleigh (1946). They noticed that Georgia lies at the end of the Appalachian mountain chain which acts as a funnel, permitting northern species to extend their ranges into the south. Evidence of a southward range expansion of the Whip-poor-will can be found elsewhere besides Georgia. In Alabama in 1924, the Whip-poor-will was listed as a mountain summer resident, restricted to the northeast section of the state (Howell 1924). Imhof (1976) mapped the Whip-poor-will's summer range to include areas of the Piedmont south of Birmingham, a substantial increase. Allen (1979) discussed factors contributing to the southward expansion of many species, and considered changes in land use to be significant in causing the Whip-poor-will's range expansion. From 1920–1940, cotton fields were abandoned in north Georgia and have subsequently produced extensive areas of forest. By 1973, 51% of Clarke County was wooded, compared to 38% in 1938. Allen (1979) determined that such an increase in forested land would be favorable for the Whip-poor-will.

The results of this study tend to corroborate Allen's (1979) findings in that the Whip-poor-will was significantly more abundant in forested areas than elsewhere in the study area and was significantly more abundant in forested areas than the Chuck-will's-widow. Since the Whip-poor-will was not recorded in Clarke County as a summer resident until 1956 and not as a breeder until 1971, change in land use contributes much as a logical explanation for this recent phenomenon.

Calling activity during an eclipse.—An unusual opportunity arose to reinforce my observations on the effect of moonlight on calling when, on the night of 24–25 May 1975, a total lunar eclipse occurred. On this night 3 counts were taken: 1 starting at full moon and continuing through the waning period, 1 during the period of total eclipse, 1 starting at total eclipse and continuing through the waning period to full moon again. The contrasts between counts were dramatic. The first count started with vigorous calling typical of a moonlit night, then decreased with a total of 24 Chuck-will's-widows and 9 Whip-poor-wills. The second count yielded only 13 Chuck-will's-widows and 5 Whip-poor-wills. The singing was also noticeably less vigorous. Half-way through the final count the moon was three-quarters full, and by the time it reached the full phase there were almost too many birds to count accurately, e.g., 33 Chuck-will's-widows and 37 Whip-poor-wills.

Table 2

Number of Calling Chuck-will's-widows (CWW) and Whip-poor-wills (WPW) During the Full Lunar Eclipse of 24–25 May 1975

	Waning period			Full eclipse		Waxing period		
Stop	CWW	WPW	Moon phase	CWW	WPW	CWW	WPW	Moon phase
1	2	—	Full	1	—	2	—	Ecl.
2	2	1	Full	1	—	1	—	Ecl.
3	2	1	Full	—	1	2	—	Ecl.
4	2	2	¾	2	1	1	1	Ecl.
5	3	—	¾	—	—	2	1	¼
6	2	2	¾	1	—	2	2	¼
7	1	1	½	—	1	2	3	¼
8	—	—	½	—	—	1	2	½
9	1	—	½	1	—	2	—	½
10	1	—	¼	1	—	2	1	½
11	1	—	¼	—	—	2	1	¾
12	—	—	¼	—	—	2	2	¾
13	2	—	Ecl.	2	—	3	3	¾
14	1	1	Ecl.	1	1	2	2	Full
15	1	—	Ecl.	—	—	—	2	Full
16	—	—	Ecl.	—	—	1	2	Full
17	1	—	Ecl.	1	—	2	3	Full
18	—	1	Ecl.	—	1	1	5	Full
19	1	—	Ecl.	1	—	2	3	Full
20	1	—	Ecl.	1	—	1	4	Full
Total	24	9		13	5	33	37	

None of the other tested variables changed appreciably during this period; thus, the change in numbers of calling birds is likely related to the change in moon phase. For a complete record of the lunar eclipse counts, see Table 2.

SUMMARY

A series of call counts was taken from 13 April–23 July 1975, to determine relative abundance of Chuck-will's-widows and Whip-poor-wills in Clarke County, Georgia, and to determine how different environmental variables affected calling behavior. A 20-station route was separated into 3 general habitat types: suburban, pasture and mixed forest. Student's *t*-test was used to test differences between numbers of the 2 species in each habitat type. Analysis of variance and lsd procedures were used to test differences in numbers of 1 species between habitat types. Tests were made for correlations between numbers of calling birds and different environmental variables. Overall, Whip-poor-wills were approximately as abundant as Chuck-will's-widows in the study area. Whip-poor-wills were significantly more numerous in forested habitat than Chuck-will's-widows and the opposite was true in open habitat. Whip-poor-wills were significantly more numerous in forested habitat than in open

or suburban areas. Chuck-will's-widows were approximately equally abundant in all 3 habitat types. Change in land use from agriculture to forest is offered as a partial explanation for the south-ward range expansion of the Whip-poor-will. Of all variables tested, moon phase showed the strongest correlation with numbers of singing birds. This observation was supported by a series of counts taken during a total lunar eclipse, during which numbers of singing birds varied directly with moon phase.

ACKNOWLEDGMENTS

Carl W. Helms and Eugene P. Odum made constructive comments. Philip E. Hale reviewed the original manuscript. A. Sydney Johnson and Graham H. Brister supplied critical reviews of the manuscript and G. H. Brister supplied statistical advice. Edward Backus assisted in preparing the figures. Paula Greene typed the manuscript. To all these individuals I extend my sincere gratitude.

LITERATURE CITED

Allen, O. S. 1979. An analysis of range extensions of certain species of birds in the Athens (Clarke Co.), Georgia area. M.S. thesis, Univ. Georgia, Athens, Georgia.

Baker, W. W. and R. H. Peake. 1966. Whip-poor-will populations in the lower Piedmont of Georgia. Oriole 31:15–19.

Barr, A. J. and J. H. Goodnight. 1972. A user's guide to the statistical analysis system. Dept. of Statistics, North Carolina State Univ., Raleigh, North Carolina.

Bent, A. C. 1940. Life histories of North American cuckoos, goatsuckers, hummingbirds, and their allies. U.S. Natl. Mus. Bull. 176.

Brauner, J. 1952. Reactions of poor-wills to light and temperature. Condor 54:152–159.

Burleigh, T. D. 1958. Georgia birds. Univ. Oklahoma Press, Norman, Oklahoma.

Dillenbeck, H. L. 1967. Whip-poor-will foray. Migrant 38:41.

Harper, F. 1938. The chuck-will's-widow in the Okefenokee region. Oriole 3:9–14.

Howell, A. H. 1924. Birds of Alabama. Brown Printing Co., Montgomery, Alabama.

Imhof, T. A. 1976. Alabama birds. Univ. Alabama Press, University, Alabama.

Mengel, R. M. and M. A. Jenkinson. 1971. Vocalizations of the chuck-will's-widow and some related behavior. Living Bird 10:171–184.

Nunley, H. W. 1960. Chuck-will's-widow. Migrant 31:57–58.

Odum, E. P. 1943. Some possible range extensions in north Georgia. Oriole 8:6–8.

——— and T. D. Burleigh. 1946. Southern invasion in Georgia. Auk 63:388–401.

Steel, R. G. D. and J. H. Torrie. 1960. Principles and procedures of statistics. McGraw-Hill Book Co., Inc., New York, New York.

Tramer, E. J. 1968. A revised list of the birds of Athens, Georgia and vicinity. Oriole 38: 2–17.

SCHOOL OF FOREST RESOURCES, UNIV. GEORGIA, ATHENS, GEORGIA 30602. (PRESENT ADDRESS: ENVIROSPHERE COMPANY, 145 TECHNOLOGY PARK, NORCROSS, GEORGIA 30092.) ACCEPTED 30 JULY 1980.

Wilson Bull., 93(3), 1981, pp. 372–382

NON-DRUMMING MALES IN A RUFFED GROUSE POPULATION

Gordon W. Gullion

The drumming display of male Ruffed Grouse (*Bonasa umbellus*) and persistent use of easily identified sites for this purpose (site association) has provided a basic population parameter for many studies of this species in recent years. This display has been a basis for extensive population inventories (Petraborg et al. 1953, Hungerford 1953, Dorney et al. 1958, Ammann and Ryel 1963, Porath and Vohs 1972), for studies of survival (Frank 1947, Hardy 1950, Dorney and Kabat, 1960, Gullion and Marshall 1968, Rusch and Keith 1971, Stoll et al. 1979), for studies of response to habitat change (Gullion et al. 1962; Doerr et al. 1970; Gullion 1970a, 1977; Boag 1976) and as a basis for judging the influence of various extrinsic factors upon populations of these birds (Gullion 1970b, 1970c; Rusch and Keith 1971; Fischer and Keith 1974; Rusch et al. 1978). The underlying assumption in these studies is that most, if not all, male Ruffed Grouse engage in this display during the peak of the spring drumming season each year, or at least that a relatively constant percentage of birds do so each season.

Earlier papers (Dorney et al. 1958, Gullion 1966) have documented that the percentage of site-associated males which can be heard in the drumming display is not constant from year to year. Furthermore, my 1966 paper agreed with the findings of Eng (1959) Dorney and Kabat (1960) and Rusch and Keith (1971) that a number of males not associated with a definite display site are usually present in the population.

The size of this non-drumming segment is an important consideration in any work dealing with Ruffed Grouse densities or population fluctuations since each male (both drumming and non-drumming) appears to represent an equal number of females in the breeding population. The work of Bump et al. (1947:516), Gullion and Marshall (1968:141) and Rusch and Keith (1971:816) indicates that the sex ratio is essentially 1:1 as the breeding season commences.

The purpose of this paper is to document the variations in the size of the "non-drummer" and presumably non-territorial component of a Ruffed Grouse population in east-central Minnesota from 1959–1978. In the context of this paper, the non-drummer is a male Ruffed Grouse which could not be identified as an occupant of a known drumming activity center and who is believed to have been a non-territorial bird for 1 or more seasons (spring and fall are each considered 1 drumming season). While there may

be some question as to whether or not drumming constitutes territorial defense, in the context of this paper I consider male grouse associated with particular display sites (i.e., drumming logs) for several weeks or months to be occupying a territory. Since active defense of a well defined territorial perimeter has not been demonstrated for this species I prefer to call these occupied areas "activity centers." The fairly even, predictable spacing (normally about 200–250 m apart) of occupied centers usual in good, homogeneous habitat strongly suggests that drumming is a mechanism for spacing and at least partially territorial in function. As used here the term non-drummer does not include males which were identified as occupying specific activity centers but which were not heard drumming during the period when most other site-associated males were actively drumming.

METHODS

Data for this paper were collected during a long-term study of the impact of forestry practices upon a grouse population that began in 1956 and is continuing on the Cloquet Forestry Center of the University of Minnesota. The area and the procedures used have been adequately described elsewhere (Gullion 1965, 1966, 1967; Gullion and Marshall 1968). The terminology concerning drumming activity used here has also been defined previously (Gullion et al. 1962; Gullion 1966, 1967) and has been used by subsequent authors (cf. Boag and Sumanik 1969, Archibald 1975, Boag 1976, Stoll et al. 1979).

In this study, we recorded activity on about 2300 drumming logs in several hundred activity centers performed by over 1200 banded male Ruffed Grouse on a study area which has varied over the years from 13–37 km^2. Numbers of occupied centers varied from 61 in 1964 to at least 254 in 1970–71. Each spring we have attempted to identify every male grouse associated with a drumming log (by trapping or reading colored leg band codes) and our success has varied from 90% in 1961 (among 144 established males in a 17.8 km^2 area) to a low of 54% in 1968 (171 established males on a 37 km^2 area).

I have drawn on information collected from the entire Cloquet study area. However, the population specifically considered in this paper is that on the 13 km^2 Cloquet Forestry Center.

In this study, we classify Ruffed Grouse as immature from the time the 8th primary is completely grown in the post-juvenal molt until they are 1 year old (the following June); as yearlings, 12–23 months of age; and as adults, 24 months and older. Birds which have molted their juvenal 9th and 10th primaries before being handled the first time are segregated in a special category of adults, since some may be less than 24 months old. These age classes differ from those used by some other authors (cf. Dorney and Kabat 1960, Rusch and Keith 1971).

RESULTS

There are 4 sources of evidence for a population of non-drumming males in a Ruffed Grouse population. One is a group of birds I have called "alternate drummers" (Gullion 1967:92). These are birds which appear to be secondary birds associated with specific activity centers, although they are not site-associated and are not heard drumming. They would be missed

in population inventory procedures based upon drumming activity or log occupancy.

A second indication of the presence of non-drumming males is the existence of young male grouse which were banded during summer and fall lily-pad trapping, and were later determined to have been alive during subsequent drumming seasons, but were not identified as drumming birds. For an individual to be included in this category there had to be evidence that the bird in question had been present in areas where all known site-associated males were identified during the period this bird was alive. Third, information was obtained by using the lily-pad trapping technique during the April–May drumming season to capture males not associated with drumming logs.

The fourth segment of the non-drumming component is comprised of unbanded yearling and adult males either appearing on logs for the first time in centers where there was no indication of activity the previous season, or as replacements for males which were identified the year before but subsequently killed. While there is some possibility of birds moving into the area from outside, our 22 years of data concerning Ruffed Grouse mobility indicate that this factor is of little consequence. From 120 records of movements by males from fall or wintering areas to drumming logs the mean distance moved was 436 m; only 11 records indicated movements of over 1 km. Also, emigration from the area would be as likely as immigration. From 1959–1976 we monitored and trapped at all of the drumming activity centers in a 400 m wide buffer zone around the Cloquet Forest as intensively as on the Forest in order to determine the extent of egress and ingress. Movement of adult male grouse was found to be slight.

Male Ruffed Grouse sharing an activity center in "satellite" status are considered territorial, drumming males in this analysis. Birds in this group are usually immatures and are always nearly identical in size to the primary drummer whose activity center they are sharing. This represents 2 male grouse in 1 activity center, and complicates population determinations based on occupied activity centers. These birds have to be counted as drumming, territorial birds since they often engage in drumming duels with the primary bird and are certain to be heard during inventories of drumming grouse. Logs used by satellite males are usually within 10–30 m of the log occupied by the primary male.

Fig. 1 shows the fluctuations in numbers of both drumming and non-drumming male Ruffed Grouse on the Cloquet Forestry Center from 1959–1978 (and drumming bird numbers to 1979). Also shown is the variation in year-to-year survival among territorial drumming males during this period.

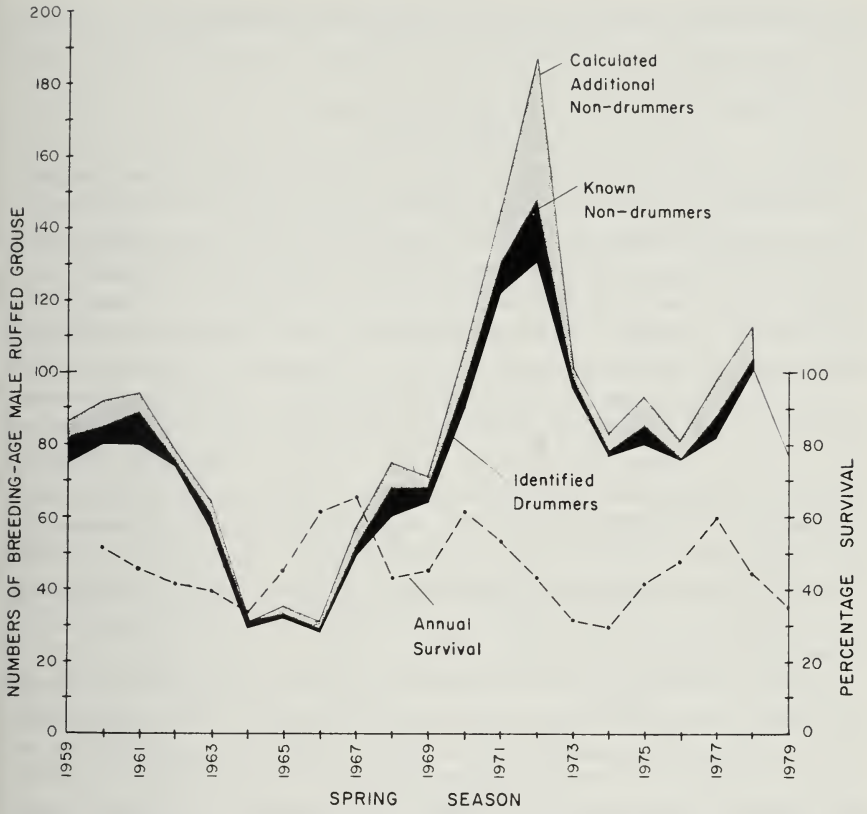


FIG. 1. Numbers of identified and known active drumming and non-drumming male Ruffed Grouse on the Cloquet Forestry Center, 1959–1979.

The figures for non-drumming males were based on the following computations. The numbers of known, banded non-drummers and alternate drummers present in the population were taken at face value, i.e., 5 banded males known to be in the population in April but not associated with a drumming log. For birds banded in the fall but not appearing on drumming logs the following season I used the annual survival rates for immatures during their first 6 months and adult survival rates for the remainder of the time (see Gullion and Marshall 1968 and Fig. 1 this paper). These 3 groups are the "known non-drummer" portion in Fig. 1.

The "calculated non-drummer" fraction was determined by applying the survival rate of the preceding year to the number of unbanded adults that appeared on logs. That is, if the 1962–63 survival rate among estab-

lished drummers was 50%, and 6 unbanded adults appeared on logs in 1963, the number of "calculated non-drummers" present in 1962 would have been 12.

DISCUSSION

The presence of non-displaying and presumed non-territorial males is known among some Tetraonidae. The Red Grouse (*Lagopus lagopus*) studies in Scotland (Jenkins et al. 1967, and others) have consistently shown an excess of males which are non-territorial and usually relegated to a surplus which dies or emigrates fairly quickly. Hoffman and Braun (1975) reported the existence of non-territorial sub-adult males in a Colorado White-tailed Ptarmigan (*Lagopus leucurus*) population and Ellison (1971) documented the existence of a non-territorial segment in a Spruce Grouse (*Canachites canadensis*) population in Alaska. The work of Bendell and his co-workers (Bendell and Elliott 1967, Zwickel and Bendell 1967, and others) has shown that a non-territorial immature (yearling) segment is an integral part of the Blue Grouse (*Dendragapus obscurus*) population structure. Among Blue Grouse, immature males have little opportunity to hold territories unless substantial new habitat becomes available through habitat modification (Redfield 1974) or a population of established birds is destroyed (Zwickel et al. 1977).

Among the lekking grouse the identification of non-displaying males is somewhat more difficult due to the daily fluctuations in lek attendance. While recognizing the problems associated with this fluctuating lek attendance in Sage (*Centrocercus urophasianus*) and Sharp-tailed (*Pediocetes phasianellus*) grouse and the Greater (*Tympanuchus cupido*) and Attwater's (*T. c. attwateri*) prairie chickens none of several studies of these species in the 1930–1950 period suggested the presence of a non-territorial segment in the male population (cf. Lehmann 1941, Grange 1948, Patterson 1952, Ammann 1957, Baker 1953). However, Robel (1969) documented the existence of a non-territorial component among lekking Black Grouse (*Lyrurus tetrix*) populations in Scotland and Rippin and Boag (1974) have found the same to be true in an Alberta population of Sharp-tailed Grouse.

Ruffed Grouse seem to be intermediate in status. Young male Ruffed Grouse frequently become established as territory holders when only 4 months old. In 1970, 24 (27%) of 87 territorial male grouse on the Cloquet Forest were on new logs where we had never recorded drumming activity previously. Ten of these were adults drumming for the first time, while 7 of 14 immatures on new logs evidently had commenced using their respective logs as 4- or 5-month-old birds in the fall of 1969. If large enough, young males may even displace older established males, forcing the latter

to move to other, usually inferior sites (Dorney and Kabat 1960:19; Gullion 1967:95, 1970d:76).

It cannot be said that the large number of non-drummers at Cloquet in the 1971–72 period represented birds which could not find suitable sites for drumming. In this period, there were at least 17 activity centers in relatively static habitats on the Cloquet Forest which had been acceptable to drummers in the 1960–1962 period, but which were not occupied by the non-drummers in the 1971–72 period. This is all the more interesting when one considers that 33% (29) of the males on the Cloquet Forest in 1970 were crowded onto 86.2 ha of 13–25-year-old aspen (*Populus*) regeneration (6% of the forest area), at a density of a male per 3.0 ha (or 33.6/100 ha). One can speculate that in this prime cover the non-drummers preferred to await their turn to occupy an activity center rather than use the poorer quality habitat that had been acceptable as drumming cover a decade earlier (see below).

Some birds never become drummers. Bird 188 was banded as a chick in August 1969, and then killed by a hunter in October 1972, 2.4 km from where he was trapped, without being associated with a drumming log. Two other birds, 1372 and 1374, both banded as young males in November 1970, were recaptured in both 1971 and 1972, but never appeared on a drumming log. In 1971, 1372 was 620 m from where he was originally banded, and in 1972 only 220 m from his 1971 location. Bird 1374 was retaken at the site of his original trapping in the fall of both 1971 and 1972, and was found as a predator kill only 164 m distant in May 1973.

A male associated with a drumming log may rarely relinquish his territory and become a non-drummer. Bird 319 was an active drummer only in 1957 and then deserted his log and activity center, and was last seen alive 1530 m distant on 22 December 1960. Bird 2123 used a log in both 1966 and 1967, then was replaced and not subsequently associated with a known log, although he was seen alive on 29 April 1971, 1520 m distant from the log he occupied earlier. Territory abandonment seems to be unusual however, for among the records for more than 1200 site-associated males only these two are known to have acted in this manner.

The Cloquet Forest has undergone considerable change in the past 25 years and this change has affected the abundance and distribution of these male grouse. Sizeable tracts of mixed conifer-hardwood forest little used by Ruffed Grouse were changed to open, unoccupied, clear-cut areas, which within 10–12 years developed into excellent aspen sapling habitat (with displaying male densities of 24/100 ha). During this period other aspen tracts in almost continuous use for as long as 15 years matured and were no longer acceptable habitats for drummers. Other habitats in less

dynamic, mixed aspen-conifer forest types have remained fairly constantly occupied at lower densities throughout the past quarter century.

These habitat changes have had some obvious effects upon the Ruffed Grouse population, as seen in Fig. 1. For example, the lowest population level during the 1974–1976 "cyclic" decline stood at 95% of the highest peak population in 1960–61, and 2.7 fold above the 1964–1966 lows. The number of drumming, site-associated males in 1972 was 1.6 times larger than in 1960–61, and there were at least 6.5 times as many non-drumming males in the population.

It appears to me that much of this increase was the result of more secure habitat being available in 1972 as compared to 1961. In the earlier years the established drummers not only occupied the best quality habitats available to them, but also occupied many sites which we now consider to have been sub-marginal. Some individual grouse survived for as long as 5 years in these sub-marginal coverts. Only a few activity centers were adequate to allow the sharing of resources between a primary and a non-drumming occupant. Young birds that could not fit into that system were lost from the population, one way or another.

As the forested lands cut over in the 1950's began to develop into acceptable coverts in the early 1970's (Gullion 1972:19) the increased numbers of territorial males showed marked shifts in the type of habitats used (Gullion 1970c:108). Additionally, a greatly increased number of non-drumming males survived in these better habitats awaiting their opportunity to occupy an activity center.

These changes may also have altered the perceptions of young Ruffed Grouse concerning habitat quality. This is reflected partly by their unwillingness to occupy vacant activity centers in areas of essentially static habitat which had been acceptable to earlier generations. Instead, many chose to await their turn to occupy a territory in this newly developed superior habitat.

Male Ruffed Grouse increase significantly in weight and size (unpubl. data) from their first to second year which means that if they are in cover which allows another season's growth their larger size places them in a better competitive position for occupying a drumming log and activity center. Five of 6 banded non-territorial males on the Cloquet area in the spring of 1970 occupied activity centers in 1971. But only 2 of the 9 banded non-drumming birds in 1971 were established in activity centers for the 1972 season. Among the 13 banded non-drummers in 1972, 5 occupied centers in 1973.

It may be that losses among the non-drumming component are greater than among the activity center occupants. This is probably true among young grouse moving into inadequate habitats during their first fall and

winter. Losses among young males which are cohabiting with site-associated males in satisfactory habitats do not appear to be greater than among the drummers. Elsewhere we have shown that drumming males associated with perennially-used drumming logs have significantly shorter survival than those on "new" logs (Gullion and Marshall 1968:132). At least 19 non-drumming males who lived for 2 or 3 years before they occupied logs lived longer than many drummers from the same cohort.

Among these 19 banded non-drummers which were finally successful in occupying activity centers 11 survived less than 12 months longer, 3 survived less than 2 years, 3 survived less than 3 years and the last 2 less than 4 years.

The data presented here do not agree with the findings of Rusch and Keith (1971:809) that the number of non-drumming males is inversely proportional to the size of the population. Data from this Minnesota study indicate the opposite: the lower the population the smaller the proportion of non-drumming males. But as noted earlier (Gullion 1966:726), the lower the population the greater the proportion of site-associated males who are not likely to be heard drumming. The presence of these birds can be determined, however, by the signs they leave at their logs and by trapping (Gullion and Marshall 1968:128).

For the biologist attempting to quantify Ruffed Grouse populations this non-territorial component presents a problem, since it can only be detected through intensive and expensive trapping and banding activities. But consolation lies in knowing that the greatest error in making inventories occurs when Ruffed Grouse are most numerous, and the least error when these birds are most scarce.

Insofar as population processes are concerned, these non-drumming birds appear to provide "momentum" to the population upswing at a time when annual survival of adult males is declining sharply (Fig. 1). During the 1970–1972 period when annual survival declined from 61.3 to 43.3% among site-associated males, the overall population continued to rise. When survival of drumming males dropped in the 1972–1974 period it was this portion of the population that filled some of the vacancies left by the death of established males and buffered the rate of adult male decline. This non-drumming population from the 1971–72 period was then at least partly responsible for maintaining the population at a higher level during the ensuing years than would have been sustained had it not been present.

SUMMARY

A non-drumming and presumably non-territorial component is a persistent characteristic of male Ruffed Grouse populations on the Cloquet Forestry Center in east-central Minnesota. Based upon a 23-year study involving more than 1200 banded male grouse using in excess

of 2300 drumming logs, it was found that the non-drumming component was least when the Ruffed Grouse population was lowest and greatest when the population reached peak abundance. During the 1972 period of peak abundance there was at least 1 non-drumming male grouse for every 2.3 known drumming grouse on this 13 km^2 study area. A change in the quality of available habitats resulting from earlier logging resulted in a marked increase in the density of drumming male grouse in this forest. Also, there was an apparent change in what male grouse perceived to be acceptable habitat for drumming. Although at least 17 activity centers (i.e., territories) in relatively stable forest situations which had been used earlier remained available and vacant, the non-drummers chose to await their turn in better quality habitats. Survival among this non-drumming component of the male Ruffed Grouse population equalled or exceeded that of birds successfully established in activity centers as drumming males.

ACKNOWLEDGMENTS

This is paper 11,435 Scientific Journal Series, University of Minnesota Agricultural Experiment Station, St. Paul, 55108, reporting progress on the Forest Wildlife Relations Project (83H). This project is funded by the Experiment Station, with supplemental funding by the Ruffed Grouse Society and the Minnesota Department of Natural Resources.

More than 240 research assistants, students and interns have participated in developing the data base for this report. I am grateful to all for their assistance. I especially want to acknowledge the long continuing encouragement and support of Drs. William H. Marshall, Milton W. Weller and A. C. Hodson.

LITERATURE CITED

Ammann, G. A. 1957. The prairie grouse of Michigan. Michigan Dept. Conserv., Game Div.

——— and L. A. Ryel. 1963. Extensive methods of inventorying Ruffed Grouse in Michigan. J. Wildl. Manage. 27:617–633.

Archibald, H. L. 1975. Temporal patterns of spring space use by Ruffed Grouse. J. Wildl. Manage. 39:472–481.

Baker, M. F. 1953. Prairie Chickens of Kansas. State Biol. Surv., Univ. Kansas Misc. Publ. No. 5, Lawrence, Kansas.

Bendell, J. F. and P. W. Elliott. 1967. Behaviour and the regulation of numbers in Blue Grouse. Can. Wildl. Serv. Rept. Ser. No. 4.

Boag, D. A. 1976. Influence of changing grouse density and forest attributes on the occupancy of a series of potential territories by male Ruffed Grouse. Can. J. Zool. 54:1727–1736.

——— and K. M. Sumanik. 1969. Characteristics of drumming sites selected by Ruffed Grouse in Alberta. J. Wildl. Manage. 33:621–628.

Bump, G., R. W. Darrow, F. C. Edminster and W. F. Crissey. 1947. The Ruffed Grouse: life history, propagation, management. New York State Conserv. Dept.

Doerr, P. D., L. B. Keith and D. H. Rusch. 1970. Effects of fire on a Ruffed Grouse population. Proc. Ann. Tall Timbers Fire Ecol. Conf. 10:25–46.

Dorney, R. S., D. R. Thompson, J. B. Hale and R. F. Wendt. 1958. An evalution of Ruffed Grouse drumming counts. J. Wildl. Manage. 22:35–40.

——— and C. Kabat. 1960. Relation of weather, parasitic disease and hunting to Wisconsin Ruffed Grouse populations. Wisconsin Conserv. Dept., Tech. Bull. No. 20.

Ellison, L. N. 1971. Territoriality in Alaskan Spruce Grouse. Auk 88:652–664.

Eng, R. L. 1959. A study of the ecology of male Ruffed Grouse (*Bonasa umbellus* L.) on the Cloquet Forest Research Center, Minnesota. Ph.D. thesis, Univ. Minnesota, Minneapolis, Minnesota.

Fischer, C. A. and L. B. Keith. 1974. Population responses of central Alberta Ruffed Grouse to hunting. J. Wildl. Manage. 38:585–600.

Frank, W. J. 1947. Ruffed Grouse drumming site counts. J. Wildl. Manage. 11:307–316.

Grange, W. B. 1948. Wisconsin grouse problems. Wisconsin Conserv. Dept., Publ. 328.

Gullion, G. W. 1965. Improvements in methods for trapping and marking Ruffed Grouse. J. Wildl. Manage. 29:109–116.

———. 1966. The use of drumming behavior in Ruffed Grouse population studies. J. Wildl. Manage. 30:717–729.

———. 1967. Selection and use of drumming sites by male Ruffed Grouse. Auk 84:87–112.

———. 1970a. Ruffed Grouse investigations—influence of forest management practices on grouse populations. Minnesota Dept. Conserv., Game Res. Quart. Rept. 30:104–125.

———. 1970b. Factors affecting Ruffed Grouse populations in the boreal forest of northern Minnesota, USA. Proc. VIII Int. Congr. Game Biol., Finnish Game Res. 30:103–117.

———. 1970c. Factors influencing Ruffed Grouse populations. Trans. N. Am. Wildl. and Nat. Resour. Conf. 35:93–105.

———. 1970d. Ruffed Grouse investigations—population dynamics and mobility. Minnesota Dept. Conserv., Game Res. Quart. Rept. 30:63–87.

———. 1972. Improving your forested lands for Ruffed Grouse. The Ruffed Grouse Society, Coraopolis, Pennsylvania.

———. 1977. Forest manipulation for Ruffed Grouse. Trans. N. Am. Wildl. and Nat. Resour. Conf. 42:449–458.

——— R. T. King and W. H. Marshall. 1962. Male Ruffed Grouse and thirty years of forest management on the Cloquet Forest Research Center, Minnesota. J. Forestry 60:671–622.

——— and W. H. Marshall. 1968. Survival of Ruffed Grouse in a boreal forest. Living Bird 7:117–167.

Hardy, F. C. 1950. Ruffed Grouse studies in eastern Kentucky. Kentucky Div. Fish and Game, Fed. Aid Proj. 18–R, Prel. Rept.

Hoffman, R. W. and C. E. Braun. 1975. Migration of a wintering population of White-tailed Ptarmigan in Colorado. J. Wildl. Manage. 39:485–490.

Hungerford, K. E. 1953. A Ruffed Grouse drumming count technique for northern Idaho conditions. Univ. of Idaho, Forest, Wildl. and Range Exper. Stat. Res. Note 10.

Jenkins, D., A. Watson and G. R. Miller. 1967. Population fluctuations in the Red Grouse *Lagopus lagopus scoticus*. J. Anim. Ecol. 36:97–122.

Lehmann, V. W. 1941. Attwater's Prairie Chicken—its life history and management. U.S.D.I. Fish and Wildl. Serv., N. Am. Fauna 57.

Patterson, R. L. 1952. The Sage Grouse in Wyoming. Wyoming Game and Fish Comm., Cheyenne, Wyoming.

Petraborg, W. H., E. G. Wellein and V. E. Gunvalson. 1953. Roadside drumming counts, a spring census method for Ruffed Grouse. J. Wildl. Manage. 17:292–295.

Porath, W. R. and P. A. Vohs, Jr. 1972. Population ecology of Ruffed Grouse in northeastern Iowa. J. Wildl. Manage. 36:793–802.

Redfield, J. A. 1974. Demography and genetics in colonizing populations of Blue Grouse (*Dendragapus obscurus*). Evolution 27:576–592.

Rippin, A. B. and D. A. Boag. 1974. Recruitment to populations of male Sharp-tailed Grouse. J. Wildl. Manage. 38:616–621.

Robel, R. J. 1969. Movements and flock stratification within a population of Blackcocks in Scotland. J. Anim. Ecol. 38:755–763.

Rusch, D. H. and L. B. Keith. 1971. Seasonal and annual trends in numbers of Alberta Ruffed Grouse. J. Wildl. Manage. 35:803–822.

———, M. M. Gillespie and D. I. McKay. 1978. Decline of a Ruffed Grouse population in Manitoba. Can. Field-Nat. 92:123–127.

Stoll, R. J., Jr., M. W. McClain, R. L. Boston and G. P. Honchul. 1979. Ruffed Grouse drumming site characteristics in Ohio. J. Wildl. Manage. 43:324–333.

Zwickel, F. C. and J. F. Bendell. 1967. Early mortality and the regulation of numbers in Blue Grouse. Can. J. Zool. 45:817–851.

———, J. A. Redfield and J. Kristensen. 1977. Demography, behaviour, and genetics of a colonizing population of Blue Grouse. Can. J. Zool. 55:1948–1957.

Dept. Entomology, Fisheries and Wildlife, Univ. Minnesota, St. Paul, Minnesota. Accepted 19 June 1980.

ASSOCIATION OF SYSTEMATICS COLLECTIONS PROGRAM EVALUATION

The Division of Environmental Biology of the National Science Foundation (NSF) is evaluating how the Systematic Biology and Biological Research Resources programs might better serve the systematic biology community in the U.S. Two surveys, developed by the Association of Systematics Collections (ASC) under contract with NSF, will gather data concerning the physical resources available to the research community and demographic information on the individuals who comprise the community.

The first survey, to be mailed to collection curators and managers in November 1981, will request information regarding management, financial resources available for support, services provided, and future needs of their collections. The second survey, to be mailed in July 1982, will collect data on individual systematic biologists.

If you do not receive a survey form by 15 November 1981 please write: Nancy Wert, NSF Project Coordinator, Association of Systematics Collections, Museum of Natural History, University of Kansas, Lawrence, Kansas 66045 or phone (913) 864–4867. Please indicate the taxonomic emphasis of your collection. A preliminary report of the results of the survey will be presented at the ASC annual meeting in May 1982.

Wilson Bull., 93(3), 1981, pp. 383–390

GENERAL NOTES

Behavioral implications of aberrant song of a Red-eyed Vireo.—In studies of avian social behavior, song (or other relevant stimuli, sensu Tinbergen [The Study of Instinct, The Clarendon Press, Oxford, England, 1951]) is often taken to be prerequisite to potential pairing or territorial defense. Playback experiments have been used to identify the aspects of a species' song conveying specific sorts of information, e.g., the identity and condition of the species and/or individual singer, crucial to the performance of these social activities (Thompson, Anim. Behav. 17:658–663, 1969; Emlen, Z. Tierpsychol. 28:241–246, 1971; Goldman, Auk 90:106–113, 1974; Fletcher and Smith, Auk 95:338–347, 1978; and others). Some recent theories of evolution of aspects of mating systems and use of space hold that social signals may play an evolutionary pace-setting role (Wilson, Sociobiology: The New Synthesis, Harvard Univ. Press, Cambridge, Massachusetts, 1975). This implies that certain social signals are not only sufficient, but necessary for an individual to defend a territory or obtain and keep a mate. To test whether the performance of specific species-typical social activities is necessary as well as sufficient would require experimental subjects occurring in natural field conditions, which were deficient in the social signal of interest.

The primary song of the Red-eyed Vireo (*Vireo olivaceus*) is structurally diverse and complex (Lemon, Can. J. Zool. 49:847–854, 1971; Rice, Anim. Behav. 26:527–549, 1978a) and plays an important role in natural behavioral interactions among conspecifics, including territorial defense and pair formation and maintenance (Lawrence, Can. Field-Nat. 69:47–87, 1953; Rice 1978a). Playback of its species-typical song elicits responses from territory holders that are qualitatively and quantitatively similar to behaviors seen in natural encounters (Rice 1978a; Rice, Anim. Behav. 26:550–561, 1978b).

In June 1973 I discovered a Red-eyed Vireo consistently singing a song unrecognizable to me as belonging to that species. Dr. Jon Barlow, who has recorded songs of Red-eyed Vireos throughout the range of the species, also heard this bird sing, and thought the song was grossly aberrant. Although Red-eyed Vireos occasionally mimic other species (James, Can. J. Zool. 54:1223–1226, 1976), the song did not sound like that of any other bird. Analysis of the behavioral interactions of this aberrantly singing bird provides a natural experiment on the necessity of species-typical song for successful pair formation and maintenance and territoriality in Red-eyed Vireos.

Methods.—My study area was in Kap-Kig-Iwan Park, 1.6 km south of Englehart, Ontario. The habitat comprises a forest of predominantly trembling aspen (*Populus tremuloides*) and white birch (*Betula papyrifera*) with an understory of speckled alder (*Alnus rugosa*) and beaked hazelnut (*Corylus cornuta*). A detailed description of the study area is given in Rice (Ecology 59:526–538, 1978c).

Behavioral interactions of Red-eyed Vireos and the procedure used in playback experiments are described in Rice (1978a). Briefly, experiments consisted of a 2-min pre-test period, followed by 2-min playback of song of the aberrant vireo, and then a 2-min post-test period. After a 10-min inter-trial interval the 3 periods were repeated, this time using normal song to provide a measure of the readiness of the subject to respond to a normal stimulus (Tinbergen 1951). During each 2-min period 17 variables were measured, covering aspects of rate, form and latency of song, as well as closeness and latency of approach to the speaker. These data were combined multivariately into a single response intensity score (Rice 1978b). For each experiment I present the scores for each period. To maximize precision, data from different subjects were not pooled. An instance of a test or post-test score being higher than the pre-test score is taken as possible evidence of a response to the song played during the test.

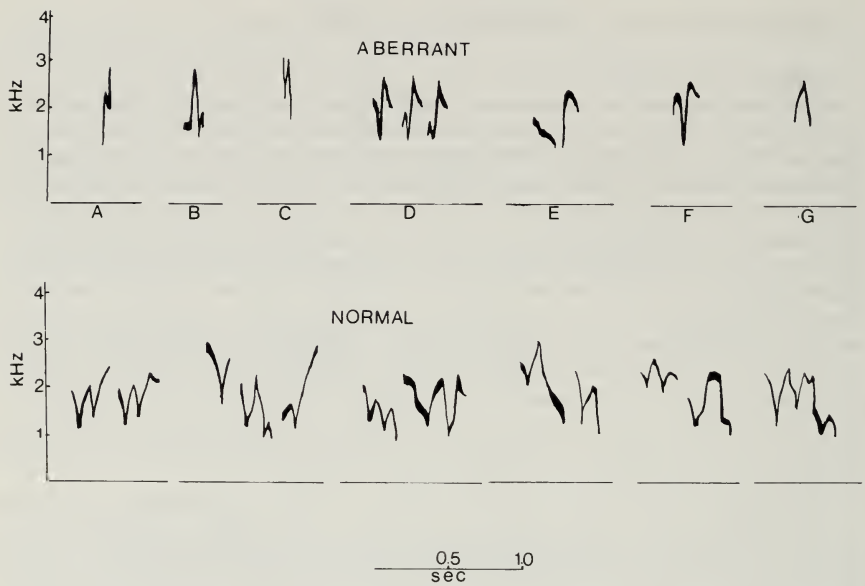


FIG. 1. Tracings of sonograms of the 7 phrases in the song of the aberrant vireo in June 1973 and 7 randomly selected normal phrases.

Results.—(1) The song. Lemon (1971) found that individual Red-eyed Vireos had repertoires of 40–60 elements, occurring either regularly in combinations or usually singly. Sequence rules for the elements and the combinations were not detectable, although extensive numbers of songs were analyzed.

Fig. 1 shows sonogram tracings of phrases of the aberrant vireo as well as some randomly chosen phrases from normal songs. The aberrant phrases are consistently shorter and less structurally complex than those depicted here or in Lemon (1971) or Rice (1978a). The 7 phrases represent all the phrases of the aberrant vireo during a 10-day recording period in June. When examined for sequencing rules, frequency of occurrence of the possible pairs of phrases deviated significantly from random (Table 1). Certain sequences, such as C-E and E-G, occurred more frequently than expected, and fewer pairs occurred than were predicted by the Poisson distribution.

(2) Playback experiments. When the playback stimulus is normal Red-eyed Vireo song scores are higher during experimental periods (test and post-test) than during pre-test control period in 11 of 20 cases (Fig. 2). Taking the response rate to normal song as a baseline rate for late June, the expected probability of an increase in response intensity during experimental periods is 0.55. After the aberrant song, 4 of 20 periods have higher scores than do their control periods (Fig. 2). The probability of obtaining a response rate this low or lower with a response rate of 0.55 is 0.002 (binomial expansion). The responses to this aberrant song by territorial vireos are significantly rarer than responses to normal Red-eyed Vireo song.

In the playback experiments with Red-eyed Vireos reported in Rice (1978a, b), 2 pre-test periods were measured during 79 trials. In these 79 trials, the response score during the second pre-test period had a 0.23 probability of being greater than the response score of the

Table 1

Transition Frequencies and Goodness of Fit Comparison to a Random Distribution for the Phrases of the Aberrant Vireo

Following phrase of pair	Preceding phrase of pair						
	A	B	C	D	E	F	G
A	—	1	0	2	1	2	2
B	4	—	0	1	1	1	3
C	4	1	—	1	0	1	4
D	0	3	0	—	1	1	0
E	0	0	11	0	—	0	0
F	0	4	0	0	2	—	0
G	1	1	0	0	5	2	—

Total of 62 phrases in 42 possible pairs of the phrases in Fig. 1 yield

No. times pair occurred	No. pairs	
	Expected from Poisson	Observed
0	9.60	17
1	14.17	12
2	10.46	5
3	5.14	2
4 or more	2.63	6

Chi square = 15.11, df = 4, $P < 0.01$.

first pre-test period. Using this as a control value for spontaneous increase in response behaviors, the probability of obtaining an increase in 4 or fewer of 20 paired 2-min trials is 0.499. The behavior of the vireos during playback of the aberrant song was not different from the behavior of vireos when no song was present. Clearly the vireos did not react to this aberrant song as if it were the song of a conspecific.

Several studies have demonstrated individual recognition of immediate neighbors (Weeden and Falls, Auk 76:343–351, 1959; Krebs, Ecology 52:2–22, 1971; Emlen 1971; Goldman 1974; Kroodsma, Condor 78:87–99, 1976; and others). All of the experimental vireos had territories distant from that of the aberrant vireo. Therefore, we cannot definitively conclude that the aberrant song played no role in territorial defense because of the lack of response in the experiments. To examine this question further the experiments were repeated with the 4 immediate neighbors of the aberrant bird.

Eight responses to 8 exposures of normal song did not differ from 6 responses to aberrant song (Fig. 3). This may reflect the small sample size. However, in the 79 experiments cited earlier there was no response to normal song in 22 instances. Using that as a measure of the normal rate of nonresponse to conspecific song, a result of 6 or more responses in 8 trials has a probability of occurrence of 0.527. The neighboring Red-eyed Vireos appeared to react to the aberrant song no differently than they did to normal song. Also, their response frequencies were those of territorial Red-eyed Vireos (in general) to normal song. The aberrant song may have functioned to restrict incursions by close neighbors.

(3) Late song. By mid-July I felt that the song of the aberrant vireo more closely resembled normal song. Sonograms of tapes of the mid-July song revealed several changes (Fig. 4). The

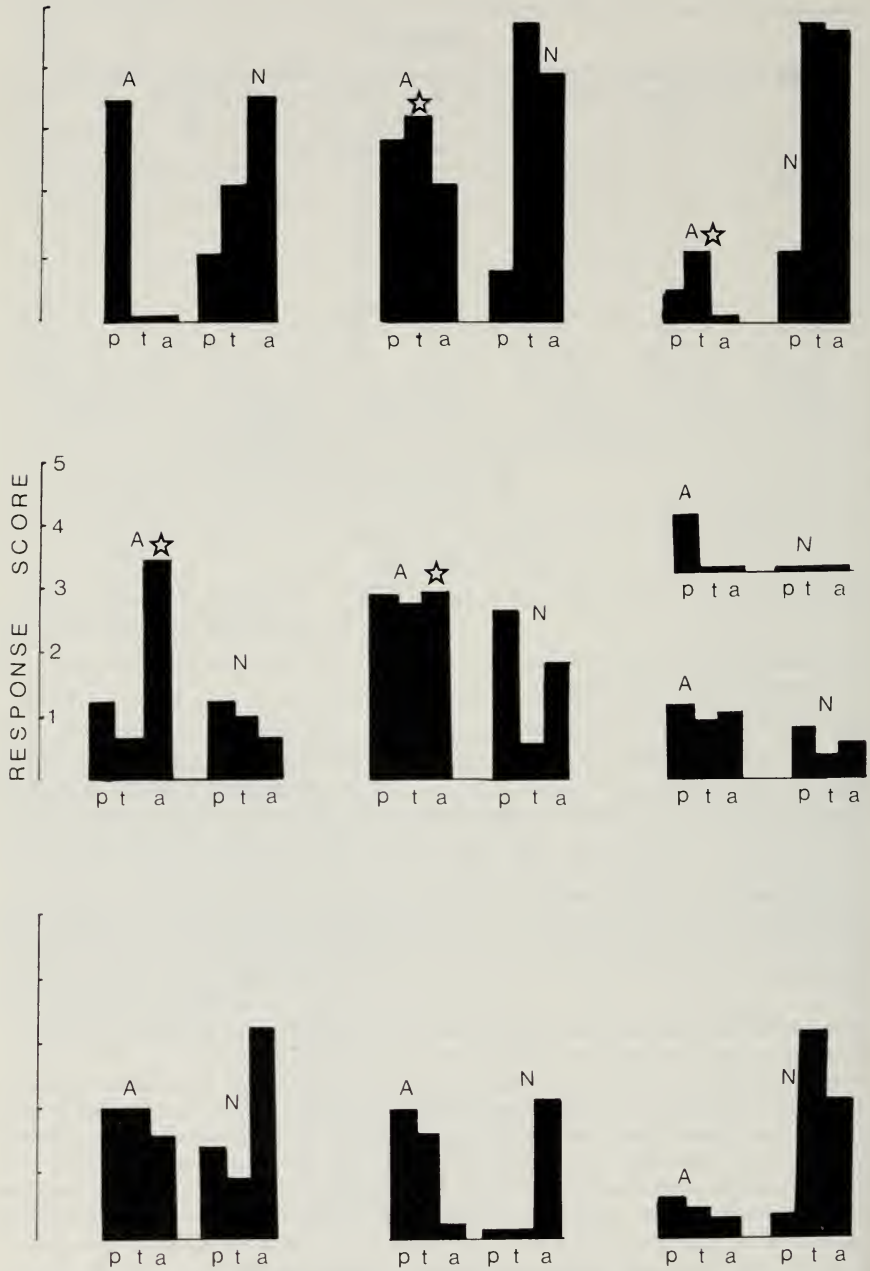


FIG. 2. Response scores for the experiments to non-neighboring territorial vireos, using aberrant (A) and normal (N) songs in June; "p" is the pre-test period, "t" the test period and "a" the post-test period; stars mark the cases where experimental period scores were higher than control period scores for tests with aberrant song.

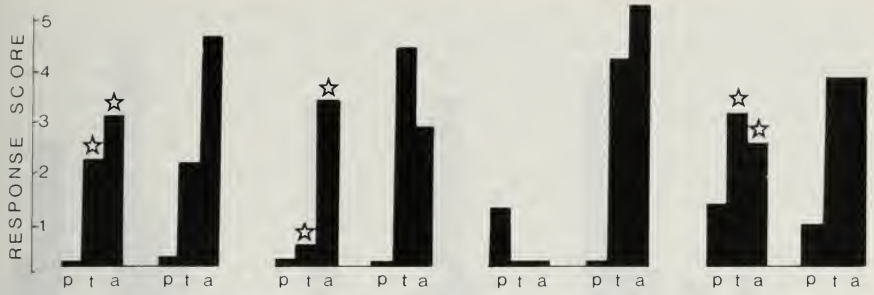


FIG. 3. Response scores for the experiments to neighboring territorial vireos using aberrant (first) and normal (second) songs. Symbols as in Fig. 2.

number of elements had increased slightly, with the addition of apparently new phrases (e.g., T) and possible differentiation of old phrases (e.g., E becoming U and Y, D becoming Z). The new phrases were more similar to those of normal Red-eyed Vireo song. The order of sequencing of phrases was also slightly less rigid than during June.

A second series of playback experiments with 9 territorial vireos was started on 14 July. By this date the rate and intensity of response to normal song is waning, but still responses can be fairly consistently elicited (Rice 1978b). The response scores of the vireos to normal song were greater in experimental than pre-test periods in 11 of 18 cases, giving a probability of response of 0.611 (Fig. 5). Increases in response scores to the late aberrant song occurred in 6 of 18 trials. With a response of probability of 0.611, 6 or fewer responses are expected with a probability of 0.02. The probability of observing the 6 or more responses under the rate of response to the earlier aberrant song is 0.14. Although the response rate has increased as predicted, the amount is not statistically significant.

(4) Natural encounters. In 39 h of observation between 14 June and 26 July 1973, I saw the aberrant vireo interact with other vireos 5 times. For other vireos with normal songs, in 125.5 h of observation over the same period, I observed 27 encounters. Also, there was no evidence of an increase in duration or intensity of encounters for the vireo with aberrant song, so the aberrant song did not make the bird appear less effective during natural encounters.

(5) Habitat quality. It is possible that this aberrant Red-eyed Vireo was occupying a territory effectively, but the territory was of inferior quality. I studied the habitat use of vireos

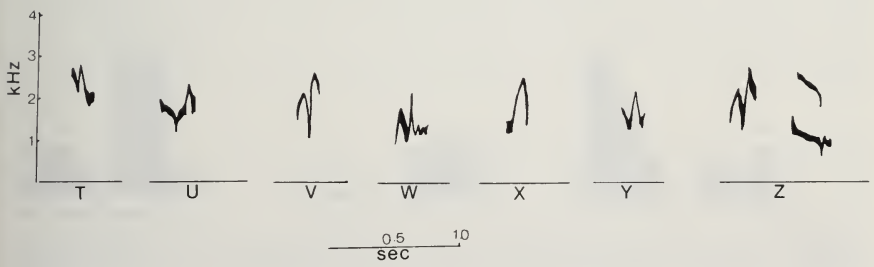


FIG. 4. Tracings of sonograms of the phrases in the song of the aberrant vireo in July 1973.

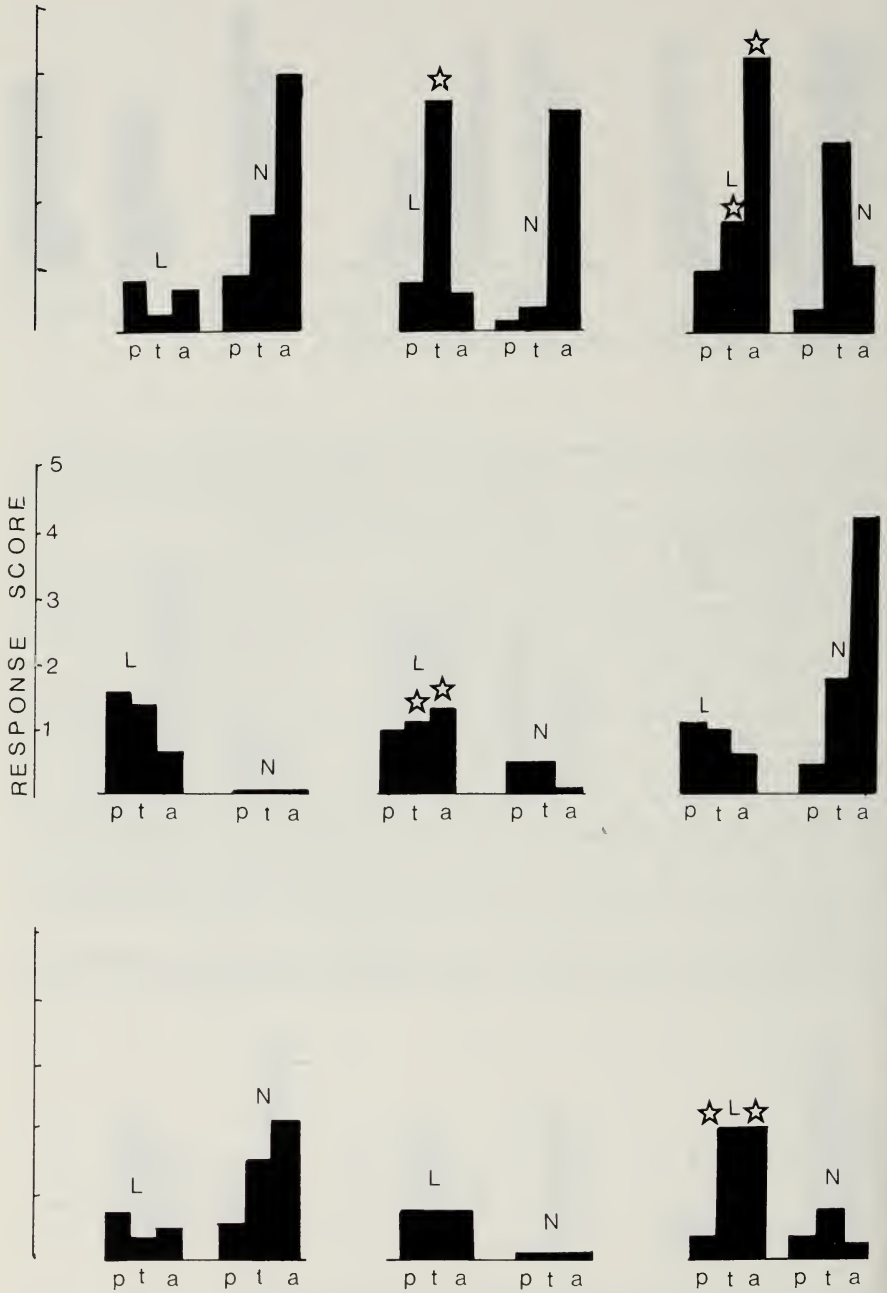


FIG. 5. Response scores for the experiments to non-neighboring territorial vireos, using late season (L) and normal song (N) from July. Symbols as in Fig. 2.

in this area in detail (Rice 1978c) and the vegetation on this territory seemed typical of most of the study area; a mature and entire aspen-white birch canopy and a fairly open alder-hazelnut understory. Quantitatively, across 3 data sets representing species composition, foliage and height distribution, and occurrence of foraging sites, 18 principal components accounted for noteworthy amounts of habitat variability (see Rice 1978c for details). The Euclidean distance of this territory score from the centroid of all 72 Red-eyed Vireo territory scores is closer to the centroids than the scores of more than 70% of all territories for each data set. This means that quantitatively the habitat occupied by the aberrant vireo is similar to the habitats occupied by the other Red-eyed Vireos in this area.

(6) Breeding success. I was not able to find the nest of this aberrant vireo, but I did see the bird frequently with a nonsinging bird and observed a variety of social behaviors, including a swaying bout (Nolan, Condor 64:273–276, 1962; Barlow and Rice, Can. J. Zool. 55:528–542, 1977). From these observations I inferred that the aberrant bird was a male and had a mate which stayed on its territory until at least 25 July.

I frequently saw the bird and its presumptive mate feeding 2 Brown-headed Cowbird (*Molothrus ater*) chicks, but no vireo chicks. However, of 13 Red-eyed Vireo pairs in the areas whose fledging success I knew for 1973, 10 fledged only 1 (4 cases) or 2 (6 cases) cowbirds, and no vireos. Thus, although there is no support for the assertion that the aberrant bird was able to breed successfully, it was no less fit than three-fourths of the Red-eyed Vireos breeding in the area.

Discussion.—There are extensive data demonstrating that species-typical song plays an important role in vireo social behavior, particularly in inter-male aggressive encounters and courtship (Barlow and Rice 1977, Rice 1978a). However, it is clear from this study that in Red-eyed Vireos the singing of a species-typical song is not always essential for the establishment and maintenance of a territory, or for obtaining and keeping a mate. In other studies as well, birds with aberrant songs have paired and sometimes bred successfully (Baptista, Z. Tierpsychol. 34:147–171, 1974; Emlen, Thompson and Rising, Wilson Bull. 87:145–179, 1975).

It is certainly possible to find specific types of information encoded in specific aspects of a species-typical song or other social signal. However, it does not necessarily follow that in the absence of any specific aspect of a song the information cannot otherwise be readily conveyed. The cost of conveying information along these alternate channels (visual displays, call notes, etc.) may be higher, but data on this point are conspicuously lacking. This vireo had both a mate and a territory typical of Red-eyed Vireos in the area, implying that the costs were not excessive and/or the alternative channels not substantially poorer. Investigators using playback experiments must bear in mind that such studies can only demonstrate that a parameter is or is not sufficient for species (or individual) recognition, not that it is necessary. Possibly for behavioral functions as important as social activities (or orientation and navigation where multiple redundant cues are also common [Schmidt-Koenig, ed., Animal Migration, Navigation, and Homing, Springer-Verlag, Berlin, West Germany, 1978]) selection favors systems of multiple cues and responses. There is a need for studies providing realistic measures of the costs of such systems, relative to their possibly substantial benefits, including opportunistic studies of naturally occurring "experiments" such as the one reported here.

Acknowledgments.—I thank Dr. Jon Barlow for coming to Kap-Kig-Iwan Park to hear this bird, for his encouragement during my research on vireos and for the loan of playback and taping equipment which had been purchased by Dr. Barlow with grant support from the National Research Council of Canada (A3472). The presentation benefitted from discussions during the Memorial University Animal Behaviour Seminars, and readings of the manuscript by Bill Montivecchi, Luis Baptista and 2 other reviewers. The cooperation of the Ministry

of Natural Resources of Ontario and the staff of Kap-Kig-Iwan Park is appreciated.—Jake C. Rice, *Dept. Biology, Memorial Univ. of Newfoundland, St. John's, Newfoundland A1B 28 Canada* and *Dept. Zoology, Arizona State Univ., Tempe, Arizona 85281.* (Present address: *Center for Environmental Studies, Arizona State Univ., Tempe, Arizona 85281.*) *Accepted 20 June 1980.*

Wilson Bull., 93(3), 1981, pp. 390–391

Courtship feeding and copulation of Royal Terns.—Although mentioned by Buckley and Buckley (Ibis 114:344–359, 1972) in their paper on the nesting of Royal Terns (*Sterna maxima*), courtship feeding and copulation have not been described for this species. These performances may occur on beaches away from islands used for nesting (Kale et al., Bird-Banding 36:21–27, 1965). Such breeding activities were apparently performed off site by the terns I studied on Cabretta and Sapelo, tree-covered islands in Georgia where they have never been known to nest. Royal Terns have, however, nested on Little Egg Island 3–10 km away (Kale et al. 1965).

My studies were made from 18–28 April 1979. It was difficult to quantify all phases of behavior since the terns were crowded in groups of from 20–200 or more, resting and preening at the water's edge.

Males, carrying a fish crosswise in their bills and making *kur-itt*, *kur-itt* notes, initiated courtship feedings by flying low over the flock, apparently to locate and alert their mates, possibly by individually recognizable "fish calls" described by Hutchinson et al. (Behavior 32:150–157, 1968) for the Sandwich Tern (*S. sandvicensis*). Transfers of fish took place in 3 situations. (1) Transfers occurring within the crowd of other terns were noted 8 times, but were interfered with twice by other terns and twice by Laughing Gulls (*Larus atricilla*) that rested among them. In the other 21 feedings or attempted feedings, the birds which were considered female (because they received food) either (2) walked out from the crowd or (3) flew to an empty part of the beach 5–10 m away.

Both birds displayed, with necks extended upward and the fore part of the closed wings held outward (Fig. 1). The female stood lower than the male, snatching the fish so quickly that display was often only momentary. The size of the fish offered appeared to be important to female selection. On 23 occasions in which the female accepted, the fish was about 7 cm in length. Of 7 refusals observed, 4 times in succession by 1 female, the fish was 5 cm in length or less and slender. When 1 male offered his mate a small fish and was refused, he walked over to offer the fish to a neighboring tern. This tern, sex undetermined, also refused. The male then returned and after several tries mounted his mate, swallowing the fish as he did so. Full copulation followed. This was the only time I observed any relation between courtship feeding and copulation.

Sometimes males and females flew to dip their bills in the waves 2–4 times. Afterwards, males flew to sea and females returned to the flock. One pair fed, then walked together in full display to the water's edge and dipped their bills in a mixture of wet sand and water 6–8 times.

Copulatory or pre-copulatory behavior, with one or more pairs performing, was so common as to be almost continuously occurring in larger flocks. Displays preceded copulations. The male, with neck extended and slightly back, and the bends of wings out like a skirt (Fig. 1), tried to walk around the female who kept turning. She often started in a low resting pose, assuming the display only as the time of mounting approached. The male held his head higher than hers, pointing his bill downward. Copulations lasted 50 sec–4 min. During nearly all of this time, males merely stood on the shoulders of the females, flapping their wings to

FIG. 1. Male Royal Tern in pose for courtship feeding.

maintain balance. The body of the female sank slightly, as her bill pointed upward. Periodically (2–3 times in longer copulations) the male worked himself near the rear of the female, coming to rest on his tarsi. He fell slightly to the right, beat his wings and maneuvered his tail under the elevated tail of the female. Cloacal contacts lasted only a few seconds. Many copulations ended with the female walking ahead, thus dumping the male. Three males and 1 female displayed briefly following copulations.

A third form of behavior was the courtship flight, similar to the "Gleitflug" described by Dircksen (J. Ornith. 80:427–521, 1932) for the Sandwich Tern. Seen only once, a pair of Royal Terns flew close together, circled high over beach and dunes and then flew out to sea where one of them floated down on the other 3 times with its wings held in a "V." Aerial displays of other terns are described by Cullen (Ardea 48:1–39, 1960).

In discussion of these observations, Buckley and Buckley (1972) distinguished drinking-skimming and feeding-skimming. Dipping of bills in the waves following courtship feedings was observed; however, this behavior appeared to be a washing of the bill to get rid of mucous left from the fish. There were, curiously, 2 points of resemblance between Royal Terns and the Swallow-Tailed Kites (*Elanoides forficatus*) whose pre-nesting behavior I watched in a preceding month (Kilham, Raptor Res. 14:29–31, 1980). Both species have unusually long copulations, the kites up to 40 sec. This may be related to both species having long wings and bodies plus relatively short legs. In both species, the male stands on the back of the female prior to holding on while sliding his forked tail under hers. Another similarity relates to courtship feeding. The females of both species demanded an offering of a definite type. With the terns this was a fish about 7 cm long and with the kites an anole (*Anolis carolinensis*) of slightly smaller size. Females of both species refused, sometimes repeatedly, other offerings. The refusals of female terns are interesting in relation to the speculations of Nesbit (Nature 241:141–142, 1973) that 1 function of courtship feeding may be to give females a chance to assess potential mates as future providers for chicks.—LAWRENCE KILHAM, *Dept. Microbiology, Dartmouth Medical School, Hanover, New Hampshire 03755.* *Accepted 10 June 1980.*

Wilson Bull., 93(3), 1981, pp. 391–392

Two cases of commensal feeding between passerines.—Observations of birds exploiting the feeding behavior of other organisms are not uncommon. Birds may use other types of animals, such as monkeys (*Macaca* sp.) (Stott, Auk 64:130, 1947) and army ants

(*Eciton* sp.) (Willis and Oniki, Ann. Rev. Ecol. Syst. 9:243–263, 1978). Numerous instances of interspecific feeding commensalism have been noted among many non-passerine birds. For instance, several cases have been documented of Snowy Egrets (*Egretta thula*) benefiting from the foraging behavior of other ardeids, mergansers (*Mergus* sp.) and terns (*Sterna* spp.) (Christman, Condor 59:343, 1957; Emlen and Abrose, Auk 87:164–165, 1970; Lamm, Condor 77:207, 1975; Bertin, Auk 94:390–391, 1977). Although the literature concerning mixed species bird flocks is extensive, the degree to which species use one another to expose or flush prey in such flocks is poorly known and controversial (Rand, Fieldiana Zool. [Chicago] 36:1–71, 1954; Partridge and Ashcroft, Condor 78:449–453, 1976).

An extensive literature search yielded only 1 observation of single or paired non-flocking passerine species exploiting one another. Willis (Ornithol. Monogr. 10, 1972) observed a commensal feeding association between Spotted Antbirds (*Hylophylax naevioides*) and Scaly-throated Leafscrapers (*Sclerurus guatemalensis*). I report 2 similar cases of this type.

On the morning of 16 March 1976, at Puerto Los Mazos near Autlán de Navarro, Jalisco, Mexico, Kenn Kaufman and I observed a pair of Rose-breasted Thrush-Tanagers (*Rhodinocichla rosea*) foraging 1–4 m apart on a sloping dry oak-forest floor at about 1385 m. They were exposing food items by flipping over leaves and other litter with sweeping motions of their bills. Accompanying them was a Fan-tailed Warbler (*Euthlypis lachrymosa*) that remained within 0.5 m of one or the other of the pair and usually perched on a branch or log above the tanagers. The warbler appeared to be using these elevated perches to see prey items exposed by the tanagers. It darted in, captured and swallowed insects exposed by 1 tanager, and then returned to the same elevated perches or others nearby. When no vantage post existed near the tanagers, the warbler observed from the ground nearby. It appeared to be successful in capturing prey uncovered by the tanagers. We were unable to determine what type of prey the tanagers and the warbler were taking; however, in over 25 min of observation we observed no conflicts between the birds. This appears to indicate that the warbler was taking prey not used by the tanagers. This warbler has also been noted following army ants in Mexico (Sutton, Condor 53:16–18, 1951; E. O. Willis, pers. comm.). As these birds moved up slope, they passed within 8 m of a Blue Mockingbird (*Melanotis caerulescens*) foraging in the same leaf-flipping manner as *Rhodinocichla*. The warbler, however, showed no interest in the mockingbird and remained with the tanagers.

While at Gedi Historical Monument (Gedi Ruins, Gedi Forest), Malindi, Kenya, on 1 July 1977, Dale, Allan and Marian Zimmerman and I observed a Red-capped Robin-Chat (*Cossypha natalensis*) closely following a Spotted Ground-Thrush (*Turdus fisheri*) foraging in dry leaf litter on the forest floor in dense understory. The thrush was uncovering food items by scratching with its feet and occasionally using the bill to toss dead foliage aside. The manner in which the chat exploited food revealed by the thrush was similar to that described above. The chat perched from 0.5–1 m above the thrush in the understory. When a food item was detected the chat flitted to the ground after the prey and then returned to its perch. This was repeated several times, but due to the dense foliage we were unable to determine the success of *Cossypha* in capturing prey. This species has also been observed exploiting the feeding behavior of elephant-shrews (Macroscelididae) in much the same manner (Rathburn, Ph.D. thesis, Univ. Nairobi, Nairobi, Kenya, 1976).

My observations are similar to those of Willis (1972) for *Hylophylax* and *Sclerurus*. In all 3 cases, the species that were exploited foraged on the ground, exposing prey by flipping leaves and other litter with their bills and/or feet. The extent to which such associations are rare or transitory vs a regular foraging strategy on the part of the follower remains to be documented.

I thank William H. Buskirk, Edwin Willis, J. V. Remsen, Jr. and J. P. O'Neill for comments on the manuscript.—Mark B. Robbins, *Louisiana State Univ., Drawer MU, Baton Rouge, Louisiana 70893.* *Accepted 1 June 1980.*

Wilson Bull., 93(3), 1981, pp. 393–394

Food finding in Black-capped Chickadees: altruistic communication?—Intraspecific flocking may increase an individual's fitness by facilitating food finding and decreasing predation. An interesting problem is whether a social bird finding a rich food source behaves selfishly or altruistically. An altruist decreases its own fitness by aiding another. A non-altruist would presumably eat without announcing the presence of food to the flock. Here I report behavior of Black-capped Chickadees (*Parus atricapillus*) on finding an especially rich food source.

From July–April in Wisconsin, Black-capped Chickadees live in flocks of 4–8 individuals of both sexes. The flocks are evidently not composed of close kin, because juveniles disperse from their natal area in July and join flocks with adults other than the parents (Weise and Meyer, Auk 96:40–55, 1979). Chickadees utter frequently the *chick-a-dee* call which may facilitate cohesion of the flock during movements (Ficken et al., Auk 95:34–48, 1978). Playback of these calls is known to attract chickadees.

This study was conducted at The University of Wisconsin–Milwaukee Field Station, Ozaukee Co., Wisconsin, over a 6-year period (1971–1977). Six feeders stocked with sunflower seeds and suet are open from mid-November–May. A total of 25 experiments was conducted (not all feeders being used each year). Most of the feeders were sufficiently spaced so that a different flock used each feeder. The birds were individually color banded; ages and sex for most birds were known. The feeders were removed each spring and replaced a day or two before being stocked with food. The chickadees did not show any attraction to the feeder site before the feeders were stocked with food. Chickadee behavior was observed as birds approached feeders stocked for the first time that season (13–17 November, depending on the year). After determining that there were no chickadees in the area, sunflower seeds were placed in the feeder. While in a blind we recorded the activities of the first chickadee to find the newly stocked feeder. If no chickadees approached the feeder within 2 h, we moved to another feeder. Observations and vocalizations were recorded with a Nagra IV tape recorder and Sennheiser MKH 104 omni-directional microphone. Vocalizations were analyzed with a Kay Elemetrics 6061B Sona-Graph.

Table 1 summarizes the results. Most birds called on finding the feeder. In 4 experiments, we were able to identify the color band code of the first bird recruited (i.e., the second bird to land on the feeder); in all cases it was the mate of the bird that called. In addition, several other flock members often accompanied the mate to the feeder. In most cases, recruitment was probably achieved through the *chick-a-dee* vocalizations. The calls given by birds finding the feeder were those typical of flocking situations, and there were no special types of calls associated with food finding. The average latency between calling and recruitment was 128 sec (±41 sec). In 2 cases, the bird finding the feeder did not call, but others were with the first bird when it arrived at the feeder and all soon began feeding. In only 1 case did a lone bird finding the feeder fail to call.

Chickadees, on finding an abundant food source, often vocalize and frequently others, particularly the mate, come to the site very quickly. Why should a chickadee attract others to a food source even if food is abundant? There would probably be costs to calling, such as decreased feeding rate if several individuals were present.

The normal winter food of chickadees is probably distributed in small packets. Chickadees show no evidence of altruism in their winter feeding away from feeders. Since chickadee flocks are not composed of close kin, a kin selection explanation of food advertisement seems unlikely. The chickadees did not cache the seeds, so a communal cache site was improbable. Reciprocal altruism (Trivers, Quart. Rev. Biol. 46:35–57, 1971) seems unlikely because membership of flocks is not very stable and the possibility of cheating is high.

The most likely hypotheses for this behavior appear to be the following: (1) It is advan-

Table 1
Finding a Recently Stocked Feeder by Black-capped Chickadees

Outcome	Frequency
No chickadees came within 2 h	15
Chickadees came within 2 h	11
Did not call within 1 min of finding feeder	3
Did call within 1 min of finding feeder	8
Another individual came within 3 min of first call-recruitment	6
No recruitment	2

tageous for an individual chickadee to be in a flock for reasons not directly related to feeding efficiency, as the flock is an effective anti-predator strategy (Ficken and Witkin, Auk 94:156–157, 1977). Therefore, it may be beneficial to share food to keep other flock members alive. (2) Chickadees are monogamous and the mate is usually in the same winter flock. It may be advantageous to be altruistic toward the mate under some circumstances (Witkin and Ficken, Anim. Behav. 27:1275–1276, 1979). (3) The cost of vocalizing on finding food may be so small compared to the advantages of this vocalization in more common contexts that natural selection has not acted to silence chickadees that discover locally abundant food (W. J. Smith, pers. comm.). Hypotheses other than kin selection to explain apparent altruism need to be tested further for the chickadee as well as other social species.

I thank R. Ficken, J. Hailman, W. J. Smith, C. Weise and S. Witkin for their criticisms of the manuscript. R. Ficken, J. Ingold, M. Plonczynski, C. Weise and S. Witkin aided in obtaining the data, and C. Weise made available data on the color banded birds. Supported by NSF grant BMS 74–19474. Publ. No. 25 of The University of Wisconsin–Milwaukee Field Station.—Millicent S. Ficken, *Dept. Zool., Univ. Wisconsin–Milwaukee, Milwaukee, Wisconsin 53211.* *Accepted 3 June 1980.*

Wilson Bull., 93(3), 1981, pp. 394–395

The sentinel crow as an extension of parental care.—In bands of feeding Common Crows (*Corvus brachyrhynchos*), some crows sit as sentinels and apparently warn feeding conspecifics of oncoming danger (Bent, U.S. Natl. Mus. Bull. 191, 1946). Other species as well make use of sentinels (Conner, Condor 77:517, 1975). Goodwin (Crows of the World, Cornell Univ. Press, Ithaca, New York, 1976) disagrees with the guardian function of the sentinel crows, citing personal contradictory observations of sentinel corvids fleeing an area before all of the feeding individuals are warned. A pair of nesting crows that we studied in the spring of 1978 may provide further insight into the actual function of the sentinel crow.

A pair of crows nested in one of a group of 14 spruce (*Picea* sp.) trees on the St. Bonaventure University campus, Cattaraugus Co., St. Bonaventure, New York. This pair was observed from hatching 4 May to fledging on 7 June. The family unit, recognizable because of aluminum leg bands on the young, was also observed in the vicinity from 7 June–7 July.

During the nesting stage, the crows were observed for 30 observation periods of 30 min each. Three main forms of antipredator behavior were observed: chasing, mobbing and nest guarding. During chasing 1 parent would fly at an intruder giving a low pitched call until the animal left the area. When the crow exhibited more intense mobbing behavior, it gave a

"rally call," and was joined by its mate and 4 other crows. The 6 crows made occasional passes at the intruder.

Guarding the nest is a less obvious form of antipredatory behavior, but is a precursor to chasing or mobbing. Guarding was not done from the nest itself but from the top of adjacent spruce trees and from deciduous trees 107 m away. Guard changes usually took place in the deciduous trees. Occasionally, the incoming crow went directly to the nest, but 82% of the time it stopped at the deciduous tree first (N = 90 of 110). The nest was only left unguarded for a mean of 1.04 times per 30 min of observation (N = 23 observations). These unguarded periods were usually brief, with a mean duration of 3.4 min (N = 24 unguarded periods observed).

After fledging, the family was seen 6 times in the adjacent woodlot between 7 June and 16 June. Since the young were not seen on the ground during this time, it was assumed that the young were still being fed by the parents. The young were not seen foraging in open fields until the first week in July. Good (Ph.D. thesis, Ohio State Univ., Columbus, Ohio, 1952) also found that fledglings do not alight in open fields until at least 2 weeks after fledging. On each occasion, when the family was seen in the woodlot, the authors were mobbed by the adults. On 2 occasions, 1 banded young tried to join in the mobbing. On both occasions, the adults began to vocalize at the young and half chased, half led the young into a tree. Once the young was concealed, the adults continued to mob the authors.

In the first week of July, the family unit under study was seen foraging in an open field adjacent to the woodlot. One adult was stationed in a nearby tree or on a fence post. The sentinel occasionally gave calls that were barely audible to an observer 100 m away. Louder calls led to the other adult joining its mate at the guard post while the 3 young continued to forage. Once when the family was approached, all 5 crows flew to the adjacent woodlot.

If these crows had not been banded and observed for the 2 months that preceded these last observations, they would have appeared as a band of feeding crows with 1 or 2 posted sentinels. Instead, we interpreted this group as a feeding family unit with 1 or 2 parents sitting on guard over the young. We feel that the sentinel is an extension of parental care originating from the guarding which occurs during nesting. The mobbing by nesting parents does not switch immediately into sentinel warning upon fledging. Instead, the parents go through a transition period in which intruders are still mobbed while the recent fledglings are being taught to flee from potential danger.

We think that sentinel crows are not altruistic, self-appointed guardians of the feeding flock. Instead, they are parent crows exhibiting antipredatory behavior as they guard their offspring. The contradictory observations by Goodwin (1976) mentioned above could be explained if the young of the fleeing sentinel were already out of danger, even if other crows were still feeding. Guarding by adults of a family would not preclude use of such sentinels by other crows, or even other species.—Gloria M. D'Agostino, Lorraine E. Giovinazzo and Stephen W. Eaton, *Dept. Biol., St. Bonaventure Univ., St. Bonaventure, New York 14778.* *Accepted 2 June 1980.*

Wilson Bull., 93(3), 1981, pp. 395–397

Behavior of a male Least Bittern incubating after loss of mate.—On 30 June 1978, I found a 4-egg completed clutch of a Least Bittern (*Ixobrychus exilis*) in a solid stand of cattails (*Typha* sp.) at Ramsayville Marsh, 4 km east of Ottawa, Ontario. The nest was located about 65 m from shore and approximately 70 cm above the surface of water ca. 40 cm deep. The nest, typical for the species (see Weller, Wilson Bull. 73:11–35, 1961), was

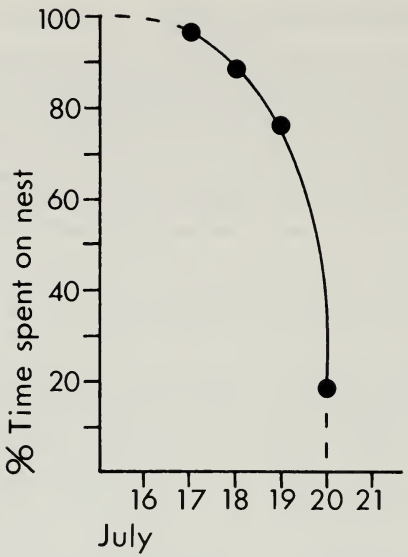


FIG. 1. Loss of interest in incubation by male Least Bittern as indicated by decrease in nest attentiveness.

supported beneath by both dead and living cattails. The latter also formed a loose canopy above the nest.

When I checked the nest on 8, 11, 13 and 14 July, either the female or the male incubated. I last saw the female on 14 July. From 17–20 July, inclusive, I observed the nest from a blind about 3 m from the nest. On 17 July, during 11 h and 35 min of continuous observation I saw the male spend 96.9% of this time on the nest, a remarkably long time since the female usually incubates more than the male (Weller 1961).

Given that 1 egg is laid per day and incubation starts with the first or second egg (Weller 1961), incubation probably began by 27 June. Since the first egg hatches 19 days after it is laid (Weller 1961), the last date for the beginning of hatching in the above nest was probably 17 July. The male attended the nest until 20 July.

While incubating, the male performed nest "jabbing" (Weller 1961) especially frequently on 18 and 19 July. He often performed the movements of picking something up and throwing it out of the nest, but nothing was seen falling except on 5 occasions when he flicked out small pieces of nesting material. Several times he suddenly got up, then vigorously pecked his feet or jabbed. After such a session, I found an unidentified arthropod in the nest. Possibly, the bittern was attempting to get rid of insects, perhaps parasites, rather than poke holes in the nest for future nest sanitation (as suggested by Weller 1961).

Each day the male's tendency to incubate was high in the early morning and waned as the day progressed, and with each day he shortened his incubation time (Fig. 1). I did not see him on 21 July (nest observed continuously from 06:45–11:20). I assumed that he abandoned the nest. On 28 July, I found the eggs cracked and carrion beetles (*Silpha* sp.) eating their contents. Since the male incubated at least 3 days beyond the latest presumed hatching date for the first egg, failure to hatch may have been due to infertility, being chilled at night or overheated in the sun.

I would like to thank all those who offered constructive criticism of this manuscript. The above observations were incidental while I was working on rails (Rallidae) in Ramsayville Marsh, a study which was supported by a Visiting Fellowship held in the ornithology section of the National Museum of Natural Sciences.—B. T. Aniśkowicz, *National Museum of Natural Sciences, National Museums of Canada, Ottawa, Ontario K1A 0M8 Canada.* (Present address: *R.R. #4, Shawville, Quebec J0X 2Y0 Canada.*) *Accepted 21 July 1980.*

Wilson Bull., 93(3), 1981, pp. 397–400

Notes on Brown Pelicans in Puerto Rico.—The biology of 2 races of the Brown Pelican (*Pelecanus occidentalis carolinensis, P. o. californicus*) of coastal United States and Baja California is well known. Few data exist for the nominate race (*P. o. occidentalis*) inhabiting the Caribbean region, especially on breeding distribution, population size and aspects of breeding biology (Wetmore, N.Y. Acad. Sci. Survey of Porto Rico and the Virgin Islands 9:245–406, 1927; Palmer, Handbook of North American Birds, Vol. 1, Yale Univ. Press, New Haven, Connecticut, 1962). A nesting colony on Conejo Cay, a 2 ha rock approximately 30 m high, near Salina del Sur Bay at 65°17′W, 18°7′N, off the southeastern shore of Vieques Island (23 km east of Puerto Rico) is easily viewed from the military operations headquarters on 190 m Cerro Matias hill, about 1 km from the colony. We spent about 15 h observing this colony from this location using a 30× telescope and 8× binocular in April–September and made other observations in Puerto Rico between March and November 1978 on 25 days in the field.

History of nesting on Vieques Island and the reason for this study.—Conejo Cay is 1 km from the impact area for air-to-surface target operations on the United States Marine Base Camp Garcia. This cay is thus subject to overflights by military aircraft on an irregular, but frequent basis and the resulting bombing and shell-fire explosions from these aircraft and from ships off-shore. On a normal bombing run the jet aircraft pass over the cay at about 400 m. We were interested in the reactions of the pelicans to these military activities.

Dr. Cameron B. Kepler first discovered the pelican colony on Conejo Cay from a Navy helicopter on 20 July 1971, and estimated 50 nests present there (Sorrie, Caribbean J. Sci. 15:89–103, 1975). These were the only data for this colony until we began a series of visits in March 1978. Local fishermen reported nesting in former years on nearby Alcatraz Rock, which is usually awash even in moderate seas. However, unless Alcatraz Rock has changed materially in recent years, which seems unlikely, close inspection suggests that it is only suitable as a roosting-loafing site.

Nesting on Conejo Cay in 1978.—Pelicans built nests on top of the island in sea grape (*Coccoloba uvifera*), limber caper (*Capparus flexuosa*), *Ipomoea* sp. and *Opuntia rubescens* from 0.5–2 m above ground. Pelicans nested on the cay from the autumn of 1977 through August 1978 with several "waves" of laying (Table 1). Most nests were established during the winter. An extended nesting cycle, with most nesting in winter, is probably typical of Brown Pelicans in the tropics (Schreiber, Auk 97:491–508, 1980). The colony was abandoned in late August–early September. Although a food shortage may have occurred, human interference probably caused the desertion. A shift in nesting location occurred during the season, with early nests formed in the middle-highest portion of the cay and later nests on the northeast edge. We were unable to determine the exact number of nests existing in the colony during 1977 and 1978. Based on the known productivity of *P. o. carolinensis* (Schreiber, Contrib. Sci. Nat. Hist. Mus. Los Angeles County 317:1–43, 1979) and the number of

Table 1

Notes on Brown Pelicans Nesting on Conejo Cay, Vieques Island, Puerto Rico, 1978

Date Observer	12 March DWB	18 May BAS	25 May DWB	1 June RWS	23 July RWS	3 Sept. RWS	22 Sept. RWS	20 Oct. RWS
Adults	60	20	26	20	13	5	0	0
Nests								
empty	[a]	0	0	0	2	6	0	0
with eggs	6	3	1	8	6	0	0	0
with naked young	1	1	2	1	0	0	0	0
downy young	1		6	10	0	0	0	0
medium size young	20	54	18	10	5	0	0	0
large young	12		6	12	6	3	0	0
dead nestlings	0	1	0	3	1	2	0	0
Flying juveniles	[a]	25+	[a]	11	19	2	0	0

[a] Present but not counted.

immature birds seen in the area, it seems likely that at least 60 nests existed from March through July; perhaps an equal number existed from November 1977–March 1978.

Clutch-size and egg-size.—Clutch-size in 7 nests on 1 June was 2.6. This figure is somewhat low since several clutches probably were incomplete. On the basis of available evidence it would appear that the clutch-size in this colony closely resembles that found elsewhere in the species (Schreiber 1979).

Eighteen eggs from 7 nests measured on 1 June and 23 July 1978 by RWS had a mean length of 73.00 ± 3.58 mm (range 67.08–79.97 mm) and a mean width of 45.40 ± 3.01 mm (range 35.15–47.90 mm). Most clutches fell within the 72–80 mm × 44–48 mm range, but 1 clutch of 2, noted as small at the time, was 69.90 × 35.15 mm and 67.08 × 44.00 mm. Eggs from Conejo Cay were significantly shorter in length ($t = 2.26$ and 2.30, df = 56, $P < 0.05$, N = 18, 39) and width ($t = 3.77$ and 5.45, df = 56, $P < 0.001$, N = 18, 39) than eggs from both the east and west coasts of Florida (Schreiber, unpubl.). They were essentially the same size as the only known preserved eggs of *P. o. occidentalis* (6 eggs in 4 clutches: $\bar{x}$ = 72.26 × 45.86 mm, range = 75.0–68.4 mm × 44.8–47.4 mm), collected from Cacachita Cay, Cuba, in September 1930 by P. Bartsch. The need for egg measurements of pelicans from the Caribbean is obvious.

Observations of the pelican colony.—On 22 July, RWS watched the colony during an air operation involving 14 jet overflights into the target region while several smoke bombs and two 500 lb bombs were exploded. During this time, 10 adults and 9 nestlings were clearly visible through a telescope in the colony. Five adults rested beside nestlings and the others sat on newly constructed nests. Pelicans are most easily disturbed during the courtship-incubation phase of nesting and if air operations were to have a noticeable effect on the adults, it should be readily apparent in these individuals (Schreiber, Ornithol. Monogr. 22, 1977).

Throughout the air operation, the nestlings continued to stand in a relaxed position, gular fluttering (Schreiber 1977). They neither moved from individual nests nor reacted obviously to the jets or bombs. The adults did not respond noticeably either. In fact, 1 pair continued

to perform low intensity courtship activity on their nest throughout the air operation. No birds took flight or moved from their nests. Three juveniles continued to swim on the water between the cay and the target range; washing, bathing and practicing normal bill plunging activities.

We believe that the Brown Pelicans nesting in this colony have acclimated to the intensive air operations. It would appear that the successful nesting during the 9 months of our studies 1977–78 indicates that these military activities have not negatively affected breeding behavior of this population.

Two incidents during our observation period on 1 June, when no jet activity occurred, are instructive. During mid-afternoon a Navy helicopter flew over the nesting island at approximately 50 m elevation. As it passed, 18 of 24 adult pelicans took flight from their nests or perches and flew in a tight circle over the colony. They returned to their nests or perches within 1 min. This response to overflying helicopter and small fixed-wing aircraft also occurs at pelican colonies in Florida (Schreiber 1977). We do not know the long term effect of such disturbance but low overflights of colonies by aircraft should be prevented. Later the same day, a 5.0–5.5 m outboard motor boat with 2 local fishermen approached the cay. Several pelicans flew from their nests or perches and circled over the island as the fishermen approached. The fishermen landed on the cay 25 m east of the nesting area at which time the remaining adults flew from their nests. The birds began to return to the area of their nests only after the fishermen departed and were 200 m from the cay. This type of human disturbance which drives adults from their nests for extended periods, in turn exposing eggs and small naked young to insolation, is precisely what causes major problems in pelican colonies. Fortunately, the naval operations in the region usually prevent such landings by local people on Conejo Cay, minimizing this sort of disturbance. Kepler and Kepler (Living Bird 16:21–50, 1977) noted similar protection by military operations in seabird colonies on Culebra, only about 20 km from Conejo Cay. Because of our study, the U.S. Navy maintains the cay as a 'no entry' zone for all military operations and restricts air traffic over and around it, thus reducing disturbance to the colony except by local fishermen.

Other observations on Vieques.—During more than 40 days on Vieques in March–September 1978 we frequently visited places along the coast where pelicans would be expected to roost and loaf. Only 2 locations were consistently used by the birds: a set of pilings on the north coast near Mosquito Pier and bushes on "Green Beach" on the west end. Both of these sites are inside the military restricted area. On most of our visists to the civilian villages we saw few or no pelicans and those birds seen were unusually wary of approach by people. We suspect this absence of pelicans and their wariness is caused by persecution and harassment of the birds by local people, either intentional or naive.

The age-class distribution of the pelicans in the loafing areas on 11 observations had a mean of 43% adults (range 38–62%), 30% subadults (range 6–38%) and 27% birds less than 1 year old (range 13–62%) (based on plumages, Schreiber, unpubl.). An age-class distribution of this composition, with a high percentage of young birds, probably indicates a stable population. We estimate that although the pelican population of Vieques comprises fewer than 200–250 birds, it is healthy and stable.

Other colonies in Puerto Rico.—Raffaele (Puerto Rico Environ. Quality Board, 1972) summarized historical records of pelicans nesting in Puerto Rico and reported that the colony on Conejo Cay was the only then known viable colony in Puerto Rico. He stated that other colonies, on islands near La Parguera and near Humacao, had recently been abandoned, apparently because of an increase in boat traffic near the islands. He noted that 4 colonies were known in the past but does not name the fourth. Perhaps it was at Caballo Blanco off Port Mulas, Vieques, mentioned by Wetmore (Auk 33:403–419, 1916). No pelicans nest on Culebra or Monito (Kepler and Kepler, 1977; Kepler, Condor 80:72–78, 1978).

Roger Zimmerman reported a colony of pelicans in Montalva Bay, near La Parguera on the southwest coast of Puerto Rico that he found on 11 February 1977 (Zimmerman, in litt.). On that date he found 25 adults on nests and 20 young ranging from 6 weeks old to fledging age, on a small mangrove island. He noted this as the only colony he found during extensive work along the southwest coast. The Montalva Bay colony apparently constitutes the only known nesting of pelicans in Puerto Rico between Kepler's 1971 aerial sightings and our 1978 observations on Conejo Cay.

Observations of the Montalva Bay colony.—RWS found 27 adults, 17 on nests, on 20 September 1978. All had brown necks, 21 had white heads but 6 had full yellow heads, indicating that courtship activity had just begun. One pair, a subadult male and full adult female, copulated while RWS was present and 2 other subadult males and 3 unsexed subadults were associated with nests. Age and sex were determined using plumage and comparative bill size (Schreiber, unpubl.). Sixteen nestlings, 4–10 weeks old were visible in 10 nests and 18 juveniles were in the immediate vicinity. This colony continued nesting activities through the fall after the Conejo Cay colony was deserted. The extended nesting season is also obvious here and the colony appeared to be the same size as was reported in February 1977 by Zimmerman.

Surveys of the pelicans of Puerto Rico.—During aerial surveys for manatees (*Trichechus manatus*) along the entire coast of Puerto Rico during 3 days each in early August, September, mid-October and November 1978, DWB counted 250, 534, 250 and 398 pelicans. These incomplete counts give a conservative estimate of the size of the total population.

A count of the pelicans in San Juan harbor on 30 October 1978, yielded a total of 350 birds, comprised of 26% adults, 7% subadults and 67% birds less than 1 year old. One-third were loafing on the tourist ship docks, one-half were in the *Casuarina* trees on the Coast Guard base, and the remainder were equally divided among the mangrove area on the southeast portion of the harbor, the channel markers and a large feeding flock. It thus appears that the Coast Guard base provides an important roost-loafing site. We suggest that the mangrove areas of the harbor are important habitat for Brown Pelicans and should be carefully protected from development and other human intrusion.

Both the Montalva Bay and Conejo Cay colonies are readily accessible and would make fine study sites for future work on Brown Pelicans in Puerto Rico. Studies on their breeding biology and on non-breeding aspects of population parameters would contribute importantly to our understanding of the marine avifauna of the Caribbean region.

Acknowledgments.—We thank Mary Margaret Goodwin and the United States Navy, M. Ralph Browning, W. Reagan, R. Zimmerman, R. Fosberg, W. Raney, W. Rushing, E. A. Schreiber, J. C. Barlow, C. Kepler, W. Robertson, M. Patrick and P. Reynolds.—RALPH W. SCHREIBER, *Natural History Museum, 900 Exposition Blvd., Los Angeles, California 90007*, DAVID W. BELITSKY, *Bureau of Land Management, Box 1869, Rock Springs, Wyoming 82901* AND BRUCE A. SORRIE, *Manomet Bird Observatory, Manomet, Massachusetts 02345.* *Accepted 9 June 1980.*

Wilson Bull., 93(3), 1981, pp. 400–403

Eggs of the Marbled Murrelet.—The Western Foundation of Vertebrate Zoology (WFVZ) recently obtained the Edward J. Booth bird egg collection from the Whatcom Museum of History and Art in Bellingham, Washington. Among the specimens in the collection is a single egg (WFVZ 113,186) which apparently is that of the Marbled Murrelet (*Brachyramphus marmoratus*).

The original account of Booth's acquisition of this specimen appeared in the Murrelet

(Anon., Murrelet 8:16, 1927) and reads in part: "Mr. E. J. Booth of Bellingham, Washington, discovered in the office of a logging camp in Whatcom County, Washington, an egg which he was unable to identify. This egg was given to him, and upon showing it to several ornithologists, including Mr. J. Hooper Bowles and Mr. D. E. Brown, it was identified as being beyond reasonable doubt that of the Marbled Murrelet. This egg had been found about fifteen miles inland, near Saxon, on the south fork of the Nooksak River, on June 19, 1925. The egg lay on a bed of moss, no nest being apparent, and incubation was about one-third advanced."

The specimen was later mentioned by Jewett, Taylor, Shaw and Aldrich (Birds of Washington State, Univ. Washington Press, Seattle, Washington, 1953), who also believed it to be an egg of the Marbled Murrelet. However, it has not been included in recent summaries of the breeding biology of the species (Binford et al., Wilson Bull. 87:303–319, 1975; Sealy, Bird-Banding 46:141–154, 1975), or has its authenticity been questioned (Drent and Guiguet, B.C. Prov. Mus. Occ. Pap. 12, 1961), perhaps because its whereabouts were not generally known.

The egg measures 58.32 × 36.51 mm with an empty shell weight of 2.222 g and a shell thickness at the waist of 0.214 mm. It is long subelliptical in shape (Preston, p. 13 *in* Handbook of North American Birds, Vol. 1, R. Palmer, ed., Yale Univ. Press, New Haven, Connecticut, 1962) and moderately glossy. The ground color of the egg is *pale glass green*, and it bears large *blackish-brown* splotches and scrawls and small spots of *gull gray*, all concentrated mostly at the larger end (italicized colors from Ridgway, Color Standards and Color Nomenclature, published by the author, Washington, D.C., 1912). Most of the spots are less than 2 mm in diameter.

In these characteristics the specimen agrees closely with indisputable eggs of the Marbled Murrelet, which now include the following: (1) an egg taken from the oviduct of a bird collected on 23 May 1897, at Howcan, Prince of Wales Archipelago, Alaska (Cantwell, Auk 15:49, 1898). Bent (U.S. Natl. Mus. Bull. 107, 1919) reproduced this egg in color (plate 48) and described it as having a *pale chalcedony yellow* ground color and being uniformly, but not thickly spotted with dark *blackish-brown* or nearly *black* spots. The egg was too badly broken to be measured accurately, but was reported to be 63 × 35 mm (Ralph *in* Cantwell 1898), which agrees closely with Bent's plate 48; (2) an egg taken from the oviduct of a bird collected on 23 May 1934, near Mittelnach, an islet in the Strait of Georgia, just east of Campbell River, Vancouver Island, British Columbia, which was described as being *pale glass green* spotted with *light lavender gray*, *deep madder blue*, *sepia*, *bone brown*, and *black* (Sutton and Semple, Auk 58:580–581 and plate 19, 1941). It measured 58.5 × 39.5 mm; (3) another oviduct egg taken on 13 July 1941, from a bird collected near Pleasant Island, SE Alaska, by Stanley G. Jewett, who stated (Jewett, Murrelet 23:67–75, 1942) that the egg agreed perfectly with the color description given by Sutton and Semple (1941) for the preceding egg, although the Alaska specimen was said to be more heavily marked. It measured 60.5 × 39.0 mm; (4) an egg photographed in a nest on East Amatuli Island, Barren Islands, Alaska, on 8 July 1978, by Theodore Simons. This egg, which was allowed to hatch, was described as being "pale olive green and covered with irregular brownish black, tar-colored spots. These spots were more prevalent around the larger end of the egg but covered it entirely." The egg weighed 41.0 g and measured 61.2 × 36.3 mm (Simons, Condor 82:1–9, 1980); and (5) another egg photographed in a nest on East Amatuli Island in July 1979 by Lee Astheimer, Katherine Hirsch and Douglas Woodby. This egg measured 58.9 × 36.3 mm and weighed 38.5 g when found; it was also allowed to hatch. I have examined transparencies of this egg, and its ground color is identical to that of the Booth specimen. However, it is more heavily spotted over its entire surface, and some of the spots are light brown, a color not found on the Booth egg.

Eggshell fragments taken from the California Marbled Murrelet nest described by Binford

et al. (1975) were identical in color to those of the Sutton and Semple specimen, except that markings of *saccardo umber* were also found. Eggshell fragments obtained with a live Marbled Murrelet from a felled hemlock tree about 0.5 miles E of Masset, Queen Charlotte Islands on about 4 June 1953 (Guiguet, Audubon Mag. 58:164–167, 174, 1956), were compared to the Jewett and Cantwell oviduct eggs in the United States National Museum by I. McT. McCowan. He found that they agreed with the latter specimens in ground color, markings and texture, and that they did not resemble eggs of the Ancient Murrelet (*Synthliboramphus antiquus*) in these details (Drent and Guiguet 1961).

An egg of the Asian race, *Brachyramphus marmoratus perdix*, was collected from a nest on 17 June 1961, by Kuzyakin (Ornithologyia 6:315–320, 1963, English translation in Josselyn Van Tyne Library, Univ. Michigan, Ann Arbor, Michigan) about 12 km NW of Okhotsk, Siberia. It is of interest that his egg differs from the North American specimens in color (blue-greenish with fine spots of brownish and hazel) and in being slightly more elongated (63.6 × 39.3 mm).

The principal distinguishing characterstic of North American Marbled Murrelet eggs appears to be their yellowish or pale green ground color. The ground color of eggs of the congeneric Kittlitz's Murrelet (*B. brevirostris*) has been described as "olive lake" (Thayer, Condor 16:117–118, 1914) or "olive-green" (Bailey, Condor 75:457–486, 1973). A series of over 100 sets of eggs of the Ancient Murrelet, the only other murrelet breeding sympatrically with the Marbled Murrelet, in the WFVZ collection have ground colors ranging from a pale cream color to rich buffy brown; none are yellowish or greenish.

In addition to the aforementioned specimens, a possible Marbled Murrelet egg was collected by Stanton Warburton, Jr., "on a mossy setting within a cavity of rocks" in a rock slide far above timberline on Mt. Doolth, Chichagof Island, Alexander Archipelago, Alaska on 13 June 1931 (Gabrielson and Lincoln, The Birds of Alaska, Stackpole Co. and Wildlife Management Inst., Washington, D.C., 1959; Drent and Guiguet 1961). A formal description of this egg has not been published, but a photograph of it is shown by Alcorn (Northwest Birds Distribution and Eggs, Western Media Printing and Publications, Inc., Tacoma, Washington, 1978). Judging from that illustration, the egg does not have a ground color characteristic of the known North American Marbled Murrelet eggs. Bent (1919) described an egg in the Charles Doe collection (now at the Florida State Museum) taken on 10 June 1904, about 70 miles N of Nome, Alaska by A. H. Dunham, which was attributed to the Marbled Murrelet and which resembles the authenticated specimens in color (*massicot yellow* with small spots of *bone brown* and *deep quaker drab*) and size (60.5 × 37.5 mm). The identity of this egg was questioned by Gabrielson and Lincoln (1959) on distributional grounds. Four eggs taken by S. J. Darcus on Langara Island, Queen Charlotte Islands on 14–15 May 1927, and claimed to be those of the Marbled Murrelet (Darcus, Can. Field-Nat. 41:197–199, 1927) are almost certainly those of the Ancient Murrelet, judging from their color and the nest descriptions. One of the latter eggs, now in the collection of the Delaware Museum of Natural History, is illustrated by Harrison (A Field Guide to the Nests, Eggs and Nestlings of North American Birds, Collins, Glasgow, Scotland, 1978).

It is therefore likely that the Booth specimen is the only whole egg specimen of the nominate race, *B. m. marmoratus*, known to have been taken from a nest. Had the nest-site from which it was collected been adequately described it would doubtless have qualified as the first North American nest of the species known to ornithology.

I am grateful to Lee Astheimer for providing me with data and photographs of the 1979 Alaska egg, to Janet Hinshaw of the Josselyn Van Tyne Library for translations of Russian manuscripts on murrelet breeding biology, and to Jon C. Barlow, Chandler Robbins and Kenneth Parkes for their helpful comments on an earlier draft. David Niles, Dana Gardner, Julie Kiff, Sam Sumida and Roger Cobb also provided help in various ways. This paper was

supported by the Western Foundation of Vertebrate Zoology.—Lloyd F. Kiff, *Western Foundation of Vertebrate Zoology, 1100 Glendon Ave., Los Angeles, California 90024. Accepted 20 May 1980.*

Wilson Bull., 93(3), 1981, pp. 403–405

First documented Cinnamon Teal nesting in North Dakota produced hybrids.—Although Cinnamon Teal (*Anas cyanoptera*) are seen in North Dakota almost every year, Stewart (Breeding Birds of North Dakota, Tri-College Center for Environmental Studies, Fargo, North Dakota, 1975) lists the breeding status as hypothetical. There is 1 unpublished record of a hen with brood sighted at Napoleon, Logan Co., on 17 July 1915, by H. H. Sheldon of the U.S. Biological Survey. However, without substantiating evidence, this sight record is unacceptable because hens and ducklings of Cinnamon Teal are indistinguishable from Blue-winged Teal (*A. discors*). There are no verified records of Cinnamon Teal breeding in South Dakota (Whitney, Harrell, Harris, Holden, Johnson, Rose and Springer, The Birds of South Dakota, The S.D. Ornith. Union, Vermillion, South Dakota, 1978), and the nearest breeding record to North Dakota is for central Montana (Skaar, Montana Bird Distribution, Bozeman, Montana, 1975) about 240 km west of the North Dakota border.

On 30 April 1978, a male Cinnamon Teal with a hen was sighted in McLean County, and observed repeatedly in the same vicinity during spring; we suspected the hen was nesting. Biologists on the study area examined all teal hens captured and on 9 June 1978, a "large-billed Blue-winged Teal hen" was trapped on a nest. This hen had characteristics of a Cinnamon Teal hen as noted by Wallace and Ogilvie (Br. Brids 70:290–294, 1977), including a more sloping forehead than a Blue-winged Teal, a darker head, a darker loral spot and a spatulated bill. The exposed culmen length was 41.9 mm which, according to Spencer (The Cinnamon Teal [*Anas cyanoptera* Vieillot]: its life history, ecology and management, M.S. thesis, Utah State Univ., Logan, Utah, 1953), placed the bird outside the range of exposed culmen lengths for Blue-winged Teal (36.5–41 mm) and within that of Cinnamon Teal (41–46 mm).

After measurements and photographs were taken, the hen was released; 6 eggs of her clutch were collected for propagation at the Northern Prairie Wildlife Research Center. Three males were raised to maturity. By early March 1979 the birds developed red-brown irises and cinnamon breast coloring similar to Cinnamon Teal, but also had partial white crescents on their heads and other plumage characteristics resembling the Blue-winged Teal (Fig. 1). The 3 males were apparently Cinnamon Teal × Blue-winged Teal hybrids. Measurements of these birds as adults compared closely with those of the 5 hybrids measured by Bolen (Wilson Bull. 91:367–370, 1979). Upper mandible lengths of the 3 hybrids were 50 mm or greater, which would fit Spencer's (1953) criterion for Cinnamon Teal (Table 1).

Crown of the hybrids were purplish iridescent resembling Blue-winged Teal, but the cheeks were a mixture of cinnamon and black flecking with facial crescents wider at the base than those of the Blue-winged Teal. Also, the crescents were not totally white but contained many red-brown feathers. The chest, belly and sides of the hybrids were cinnamon colored but contained black spots like those found on Blue-winged Teal. The hybrids had a remnant of the Blue-winged Teal flank patch but it was smaller, cinnamon colored with black flecking. There are numerous reports on Cinnamon Teal × Blue-winged Teal crosses, and those pictured by Lahrman (Blue Jay 29:28, 1971) and Bolen (1979) appear to be similar to the ones reported here. An unreported Cinnamon Teal × Blue-winged Teal hybrid collected near Wishek, McIntosh Co., on 23 May 1970, is preserved at the North Dakota Game and

FIG. 1. Male Cinnamon Teal × Blue-winged Teal hybrid (bottom) compared with a normal Blue-winged Teal male (top).

Table 1

Measurements of Cinnamon Teal × Blue-winged Teal Hybrids at Age 289 Days

Bird ID[a]	Tarsus length (mm)	Weight (gm)	Total wing length (mm)	Exposed culmen length (mm)	Upper mandible length (mm)	Upper mandible width (mm)	Wing chord length (mm)
1049	—	360	255	45	50	19	178
F500	31	370	282	45	54	18	181
F499	29	358	262	45	52	18	182

[a] Skins of birds F499 and F500 are available at the Northern Prairie Wildlife Research Center, Jamestown, North Dakota.

Fish Department Office at Bismarck. This bird is similar in plumage to ones described above, but lacks the facial crescent.

The hybrids observed here resulted either because the Cinnamon Teal female or the male were hybrids or because the female was mated to a male Blue-winged Teal. We believe that the McLean County hen was a pure Cinnamon Teal because of her bill measurements and plumage, and that she had bred with Blue-winged Teal male(s). Blue-winged Teal males were abundant in the vicinity and according to Connelly (A Comparative Study of Blue-winged Teal and Cinnamon Teal Breeding in Eastern Washington. M.S. thesis, Washington State Univ., Pullman, Washington, 1977), the more aggressive Blue-winged Teal could dominate Cinnamon Teal, particularly in certain habitats.

Nine male Cinnamon or cinnamon-like teal were sighted by North Dakota Game and Fish Department biologists during spring waterfowl surveys between 1958 and 1978 (Charles H. Schroeder, pers. comm.). Three were considered Cinnamon Teal × Blue-winged Teal hybrids. This surprisingly large percentage of hybrids, plus the production of hybrid young by an apparent Cinnamon Teal hen, may indicate that the Cinnamon Teal is having difficulty establishing itself as a pure species in North Dakota because of sexual aggressiveness of the ubiquitous Blue-winged Teal.

We thank Douglas L. Johnson for commenting on the manuscript, and we appreciate the field help of Randy Naze and Jon Anderson.—John T. Lokemoen and David E. Sharp, *U.S.D.I. Fish and Wildlife Service, Northern Prairie Wildlife Research Center, Jamestown, North Dakota 58401.* *Accepted 1 June 1980.*

Wilson Bull., 93(3), 1981, pp. 405–406

First record of the Black-chinned Hummingbird in Alberta.—The Black-chinned Hummingbird (*Archilochus alexandri*) occurs from northwestern Mexico north to southern British Columbia. It is not usually found east of the Rocky Mountains, except in the Plateau region of southwest Texas (A.O.U. Check-list Com., Checklist of North American Birds, 5th ed., Lord Baltimore Press, Baltimore, Maryland, 1957).

The black-chin is uncommon in the northern portions of its range. In Idaho, the species is distributed primarily in the northern portion of the state (Burleigh, Birds of Idaho, Caxton Printers, Caldwell, Idaho, 1972). In Montana, it is restricted to the northwest portion of the state; it breeds in the Missoula and Philipsburg regions and non-breeding individuals have been recorded farther north in Libby, Kalispell, Polson and Seely Lakes regions (Skaar,

Montana Bird Distribution, Bozeman, Montana, 1975). The species is relatively rare in Washington, occurring primarily in the eastern portion of the state (Jewett, Taylor, Shaw and Aldrich, Birds of Washington State, Univ. Washington Press, Pullman, Washington, 1953). In British Columbia, the species is limited to the southern interior of the province; its range extends east from Chilliwack to Creston and Kimberley and north to Grindrod (Godfrey, Natl. Mus. Canada Bull. 203, 1966).

On 25 June 1979, a Black-chinned Hummingbird was picked up in Calgary, Alberta; the bird had struck a window on or just prior to 25 June. This specimen, preserved as a study skin (Provincial Museum of Alberta, specimen no. Z79.143.1), was identified as a mature male by both plumage and age criteria given by Ortiz-Crespo (Auk 89:851–857, 1972). Its testes were approximately 1 × 1 mm. The specimen had very little body fat and weighed 2.9 g.

This specimen constitutes the first authentic record of the Black-chinned Hummingbird in Alberta. There are, however, unsubstantiated indications that this species was recorded in Alberta in the 1800's. Saunders (Ottawa Nat. 16:97–103, 1902) stated, without supportive evidence, that the range of this species extends east from the Pacific Ocean to the Alberta foothills, and as far north as Banff in the Rocky Mountains. Bendire (Smithson. Contrib. to Knowledge 985, 1895) includes southern Alberta within the range of this species, but placed a question mark after this statement in his text.

Several lines of evidence suggest that the occurrence of the Black-chinned Hummingbird in Alberta is accidental. Firstly, the northern limits of the Black-chinned Hummingbird's range are quite stable. The historical distribution of the black-chin in Montana (Bendire 1895; Saunders, Pac. Coast Avif. 14, 1921) is very similar to its present distribution (Skaar 1975), with the exception of a dead bird recovered in Bozeman during spring migration in 1976 (Rogers, Am. Birds 30:867, 1976). The present distribution of the species in British Columbia (Guiguet, B.C. Prov. Mus. Handbook 37, 1978) parallels its historical distribution (Brooks and Swarth, Pac. Coast Avif. 17, 1925), with the exception of a male observed at Nicholson, 8 km south of Golden (Rogers 1976). There is also a sight record for Regina, Saskatchewan (Jowsey and Jowsey, Blue Jay 28:120, 1970).

Secondly, the Black-chinned Hummingbird prefers the dry foothills and canyons of the Upper Austral Zone (Grinnell and Miller, Pac. Coast Avif. 27, 1944), a habitat type not found in the Transition Zone in southern Alberta (Hunt, Natural Regions of the United States and Canada, W. H. Freeman and Co., San Francisco, California, 1974).

Acknowledgments.—The authors extend their thanks to the Alberta Fish and Wildlife Division, particularly G. L. Erickson, for recovering and donating the specimen to the Provincial Museum. This paper is Provincial Museum of Alberta contribution number 56.—Philip H. R. Stepney and Peter C. Boxall, *Ornithology Program, Provincial Museum of Alberta, 12845 102 Avenue, Edmonton, Alberta T5N 0M6 Canada.* *Accepted 30 July 1980.*

Wilson Bull., 93(3), 1981, pp. 407–437

ORNITHOLOGICAL LITERATURE

Special Review

Old Birds and New Ideas: Progress and Controversy in Paleornithology

Papers in Avian Paleontology Honoring Hildegarde Howard. By Kenneth E. Campbell, Jr. (ed.). Contributions in Science, Natural History Museum of Los Angeles County, No. 330, 1980:xxxviii + 260 pp., numerous tables, line drawings and black-and-white photographs. $20.00 + $1.25 shipping charge. Order from the Museum Bookshop, Los Angeles County Museum of Natural History, 900 Exposition Blvd., Los Angeles, California 90007. Relationships and Evolution of Flamingos (Aves: Phoenicopteridae). By Storrs L. Olson and Alan Feduccia. Smithsonian Contributions to Zoology, No. 316. Smithsonian Institution Press, Washington, D.C., 1980:73 pp., 40 figs., 2 tables. Price not given. *Presbyornis* and the Origin of the Anseriformes (Aves: Charadriomorphae). By Storrs L. Olson and Alan Feduccia. Smithsonian Contributions to Zoology, No. 323. Smithsonian Institution Press, Washington, D.C., 1980:24 pp., 15 figs. Price not given. The Age of Birds. By Alan Feduccia. Harvard University Press, Cambridge, Massachusetts, 1980:196 pp., numerous black-and-white illustrations. $20.00.—The publication in one year of several major works in avian paleontology provides an opportunity to assess the current situation in this important subject. Included in this survey is a Festschrift volume honoring one of the field's leaders, 2 monographs that analyze both extant and fossil birds to develop provocative new phylogenetic theories and a popular volume that aims to explain the history of birds and the methods of its study to a nonspecialist audience.

Dr. Hildegarde Howard has spent over half a century studying fossil birds at the Natural History Museum of Los Angeles County. The volume edited by Kenneth E. Campbell, Jr. is a tribute to her immense contributions to the discipline and to the inspiration that she has provided to other workers. It includes "appreciations" by several colleagues and a review of her work by Campbell, who notes among Howard's major contributions her studies on the Emeryville shellmound, the asphalt deposits of Rancho La Brea, the tertiary marine birds of southern California, and the use of trinomials to designate chronoclinal variation. Her work has included not only the description of many new forms, but also extensive paleoavifaunal analyses and important reviews. Campbell emphasizes the "caution, restraint, and thoroughness in methodology" that characterizes Howard's work. A bibliography of her 140 titles from 1923–1979 is included. Also reprinted here are the detailed drawings of avian bones that first appeared in Howard's 1929 paper on the Emeryville shellmound, and which have long served as a basis for avian osteological nomenclature.

The volume contains 19 contributed papers on various aspects of paleornithology, including faunal studies, reviews of specific groups, descriptions of new forms, archeological studies, and theoretical aspects. The paper likely to cause the most comment is Joel Cracraft's critique of the application of phylogenetic theory and method in avian paleontology. Cracraft argues that the use of cladistic methods will improve systematic practices in the field; this is not a new idea. Hopson and Radinsky (Paleobiol. 6:250–270, 1980) discuss the impact of this approach on vertebrate paleontology, noting its gradual spread into the field as well as the resistance to it in some quarters. This characterizes avian paleontology as well. Some paleontologists have especially resisted the argument that fossils cannot be designated un-

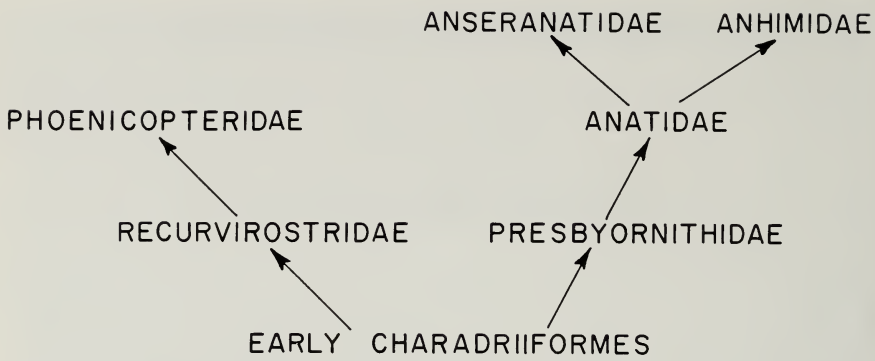


FIG. 1. An attempted reconstruction of Olson and Feduccia's theory of phylogenetic relationships in several groups of birds.

equivocally as direct ancestors of later forms. Storrs L. Olson in one paper rails against simplistic applications of cladistics, while other contributors are uncomfortable and apologetic about their continued use of phenetic methods. In my opinion, many paleontologists are overly sensitive to criticisms of their methods, but we must recognize that their data are by their nature often fragmentary, both in terms of individual specimens and of the fossil record as a whole. Part of the problem arises from incomplete fossils that lack sufficient information to allow unambiguous classification, let alone the construction of phylogenies. Much of the older literature contains taxonomic decisions that are simply not justified by the available data, which is why so much of the literature involves the reallocation of fossils to new taxa. Olson has done a major job in this area lately.

The goal of higher-level systematics is to work out the relationships between the major groups. The highest level at which presumably "natural" (monophyletic) avian groups are usually classified is the order. The problem is to work out the relationships between these orders, and this essentially must begin by determining pairs of orders that are related either as sister groups, or by having one derived from some group within another. The 2 Smithsonian Contributions by Olson and Feduccia represent major efforts in this direction involving comparative studies of both fossil and extant birds. In the first paper, the authors argue that the flamingos (Phoenicopteridae) are not related to either the Ciconiiformes or the Anseriformes as previous authors have suggested, but that they evolved from the family Recurvirostridae (stilts and avocets) of the order Charadriiformes. In the second, they argue that the Anseriformes are not closely related to the Galliformes as often stated, but have evolved from the Charadriiformes via an extinct, intermediate family Presbyornithidae. In both papers they marshall impressive arrays of data with which they evaluate alternative hypotheses. Both papers are so poorly organized, however, that it is often difficult to follow an argument through various digressions, and worst of all, there are no dendrograms summarizing the phylogenetic hypotheses being proposed; indeed these hypotheses are not clearly articulated in either paper. In the accompanying figure I have reconstructed from their texts what I believe to be Olson and Feduccia's combined hypotheses.

One problem with these papers is their confusing mixture of methods. The studies themselves are like those intermediate fossils that the authors analyze, that is, mosaics of primitive (phenetic) and advanced (cladistic) clustering techniques. The application of cladistic methods here is uncertain, however, because there is usually no explanation offered of how the

characters were determined to be derived. The connection of the Presbyornithidae to the Anseriformes is proposed on the basis of a complex shared derived cranial morphology, and appears to be well founded. However, the critical connection between the Presbyornithidae and the Charadriiformes is supported only weakly at best. Some skull characters are listed (pp. 14–15) as similarities between *Presbyornis* and Charadriiformes, but these appear to be mainly primitive avian characters from which the Anseriformes alone diverge. Thus, they do not link the Presbyornithidae to the Charadriiformes any more than to any other group of birds. The supposed charadriiform connection is also based on characters of the postcranial skeleton. These are listed on pp. 12–13, but are not discussed in detail, reference being made to 2 earlier papers by Feduccia. One (Am. Scientist 66:298–304, 1978) is a semipopular account with no real data; the basis for the connection evidently lies in the other (Auk 93:587–601, 1976). This paper simply does not provide the needed documentation for such an important hypothesis. For one thing, Feduccia claims to accept the superiority of cladistic methods over phenetic clustering, but confesses that he cannot analyze his data cladistically with much confidence (p. 599). There are few data to analyze anyway. The reader cannot determine what data were actually used; the paper has no methods section nor any list of species or numbers of specimens examined. The text refers vaguely to "recurvirostrids," "shorebirds" (=Charadrii?) and "charadriiformes," but only 1 charadriiform species (*Recurvirostra americana*) is really analyzed. There is no indication that any comparative analysis of the Charadriiformes was made. (Indeed, in this 1976 paper Feduccia had used these same few data to support a different hypothesis, namely that *Presbyornis* is ancestral to both Anseriformes and flamingos, which are sister groups in a lineage separate from that containing recurvirostrids and "shorebirds.") Ultimately, the proposed relationship between *Presbyornis* and the Charadriiformes appears to be based on some intuitive notion of general similarity, and is hardly documented in these papers. What is needed are: (1) derived characters shared by the Charadriiformes, Presbyornithidae and Anseriformes, plus, (2) additional derived states shared by the latter 2 groups. The second requirement is well met, but the first is not.

There are other difficulties. The hypothesis that Anseriformes are derived from Charadriiformes means that the often-claimed connection between the Anhimidae (screamers) and the Galliformes must be incorrect. The authors note a resemblance between screamers and the Magpie Goose (*Anseranas semipalmata*), which ties the screamers to the Anatidae. They report the discovery of a series of minute ridges in the ramphotheca of screamers; these resemble poorly-developed lamellae, and are considered homologous with those of the Anatidae. Olson and Feduccia claim that these are vestigial lamellae, and that screamers evolved from fully lamellate ancestors, with *Anseranas* being close to an intermediate stage in this trend. Here they have introduced a revolutionary view of the history of the waterfowl. Traditionally, screamers were regarded as very primitive, *Anseranas* as more advanced and the Anatidae as most advanced. Olson and Feduccia suggest instead that *Anseranas* and screamers are highly derived. This provocative thesis poses some problems. It suggests that major anatid specializations, including a spatulate bill, lamellae and simultaneous wing molt, were secondarily lost in screamers. As an argument that the feeble lamellae of screamers are vestigial (reduced) rather than primitively rudimentary, they argue that screamers are not filter feeders. Interestingly, in the flamingo paper they have provided an alternative hypothesis in another context. In discussing the evolution of bill lamellae in *Pachyptila* (Procellariidae), where different species show different degrees of development, they suggest that "the rudimentary lamellae in the less specialized filter-feeding petrels provide gaps for the expulsion of water while the prey is held in place with the tongue." Perhaps the lamellae in screamers serve similarly. Even though they are not filter feeders, they do feed on marsh plants and might have use for such drainage. Olson and Feduccia's hypothesis requires the

re-evolution of a set of primitive characters. In the flamingo paper (p. 67), they consider such a process in the Recurvirostridae to be unlikely. Should they not apply the same caution here? Another possibility is that the screamers are the sister group of the Anseranatidae + Anatidae. This would require fewer evolutionary reversals. I am not arguing one hypothesis over another here, but merely pointing out that alternative hypotheses of this sort can best be evaluated with cladograms showing the distribution of characters among taxa.

The papers by Olson and Feduccia are powerful efforts to synthesize paleontological and neobiological data so as to analyze relationships between major higher taxa. The flamingo paper is especially well argued, as it includes new fossil forms that reasonably bridge the gap between hypothesized ancestors and descendents, as well as an excellent functional interpretation of the flamingo feeding mechanism. The strengths of these papers lie in the detailed descriptive comparisons between numerous fossil and extant forms, and in their uninhibited speculations in a context of stratigraphic and functional considerations. Their weaknesses lie in their indecisive mixtures of phenetic and often poorly-argued cladistic methods, and in their failure to present their phylogenetic hypotheses in the form of dendrograms showing the proposed relationships and the characters on which they are based. In this way they could also show whether their data really allow a particular fossil form to be hypothesized as the direct ancestor of later groups; that is, whether it possesses all and only those derived characters that such an ancestor must exhibit. As noted, the designation of fossils as ancestors is a point of contention between many paleontologists and some of their critics; ultimately, it is a matter of character distribution, which can be displayed unambiguously by a cladogram. An example of the splendid work that can result from the application of rigorous analytical methods to a good fossil record is the study of the Dromornithidae by Pat Vickers Rich in the Howard Festscrift volume. Here the hypothesis is set forth precisely in a cladogram with the characters defining each node shown in the diagram and discussed in the text. This paper sets a standard to be followed in studies of this sort.

In The Age of Birds Alan Feduccia presents an account of avian evolution for the nonspecialist. He wisely chose to discuss highlights of avian history rather than getting bogged down in endless details or argument. The result is a readable introduction to the subject with a lot of familiar stories adequately retold, some interesting new material, and several irksome shortcomings. Chapter 1, "The feathered reptile," is a retelling of the *Archeopteryx* story. The point of the title is that *Archeopteryx* is a true evolutionary intermediate showing that birds evolved from "reptiles." I must insist that it is not a "missing link," however, because it is not missing. It is just a link. It is not a "reptile" either, it is a bird because it has feathers, a derived condition that defines Aves as monophyletic. Of special value is the review of the more recently discovered fossils, the Maxberg, Teyler and Eichstätt specimens. The photographs are also worthwhile; some are of the familiar London and Berlin specimens, but the newer specimens have not previously been shown in any popular account that I know of.

In chapter 2, The Ancestry of Birds, Feduccia reviews the various theories of avian origins. There is a brief mention of recent challenges to John Ostrom's popular view of dinosaurian ancestry, but nothing new is added. Chapter 3, The Evolution of Flight, carries us through a familiar tale of hypothetical behavioral stages (jumping, falling, parachuting, etc.) and organisms (Nopsca's and Heilmann's proavian dreams, Ostrom's flyswatters, baby hoatzins). As usual much of the discussion centers on the flying abilities of *Archeopteryx*, and some recent anatomical interpretations are mentioned. However, certain provocative new theories published in recent issues of the Auklet are inexplicably ignored. The topics of chapters 2 and 3 are hardly mentioned in the contributions to the Howard Festschrift, most of which have a satisfyingly high ratio of data to speculation. Chapter 4, Toothed Birds and Divers,

is mostly standard stuff (*Hesperornis*, *Ichthyornis*) with brief mention of more recent work on wing-propelled divers by Hildegarde Howard (auks) and Storrs Olson (plotopterids). Campbell gives an account of Howard's studies of both groups in the Festschrift, where Olson also has a paper on the plotopterids.

Chapter 5 is mostly devoted to an account of Olson and Feduccia's theory of relationships between flamingos, Anseriformes, Charadriiformes and *Presbyornis*, which I discussed above. Although stronger in assertion than documentation, it does provide a sort of phylogeny (p. 95) outlining some of the relationships proposed in the 2 Olson and Feduccia papers, where no such representation was given. A problem becomes apparent here that did not surface in the other papers. In earlier works Feduccia made a point that in *Presbyornis* the nasal-frontal bones are arranged in a V-shaped conformation otherwise found only in flamingos. This seemed important while he was advocating a *Presbyornis*-flamingo connection. In The Age of Birds (p. 92), Feduccia merely notes that "the flamingolike nasal-frontal region may still link *Presbyornis* and the flamingos, although their divergence was surely an ancient one." What does this mean? Is this one of those mysterious primitive charadriiform characters often mentioned but seldom documented in these works? This example illustrates the vagueness that results from the lack of a proper character analysis.

Chapter 6, The Evolution of Flightlessness, is the best part of The Age of Birds, and is the best discussion of the subject in the recent literature, analyzing both familiar examples like the ratites, and illustrating some remarkable new fossils of flightless forms, such as an extinct flightless goose from Hawaii. There is a good discussion of how flightlessness has evolved repeatedly in birds through neoteny. This is based particularly on Storrs Olson's analysis of the flightless rails (Smithson. Contrib. Zool., No. 152, 1973), an outstanding example of the use of fossils to interpret the epigenetic processes by which evolutionary change occurs. There is also a chapter on birds of prey.

The final chapter of Feduccia's book deals with the rise of land birds. This is a long and rambling survey of the major bird groups not previously covered. The fossil record does not provide clearcut evidence for relationships between major groups, and most groups are described more than analyzed. In developing a history of major groups an excessive reliance is placed on the relatively few important fossils. The chapter is characterized by unsupported statements like "Lyrebirds and scrub-birds are clearly the most primitive of the oscines." This statement has a precise meaning, namely that all oscines other than scrub-birds and lyrebirds are clustered by the possession of some derived character(s) for which the latter are primitive. Perhaps they are, but if so we should be told at this point what the characters are.

The book ends with an illustration that purports to show relationships between the Passeriformes, Coraciiformes and Piciformes. Methods now exist, through cladistic analysis, to produce precise and information-rich graphic representations of genealogy. Feduccia claims to accept the validity of this approach (e.g., pp. 151–152), and so it is difficult to understand why he would present the virtually meaningless diagram on p. 180. Most of the groups shown represent lineages that do not connect with other lineages in the diagram. Some end blindly as solid lines, others fade into dashed lines before ending in open space. The entire assemblage is clustered by 2 plesiomorphic conditions, the primitive stapes and anisodactyly, which will not even define the class Aves. The "Alcediniformes" and Trogonidae are shown as sister groups, clustered by an unusual stapes, a character discovered by Feduccia and considered derived within birds. This proves that he knows how to do it right. The suboscines and oscines are shown as sister groups, but only with dotted lines, whose meaning is not mentioned, and no characters clustering them are given (though a couple are mentioned in the text). Four other groups are shown without connections, except that they approach each other at various angles and distances, which may be intended to hint at some suspected

relationship. Some groups have no characters, others have various kinds of different value. For instance, the oscines have "derived syrinx morphology," which is good, "advanced 'passerine' morphology," which is vague, and "double fossa of humerus in advanced lines," which is irrelevant. In this example, The Age of Birds does not provide the reader with a coherent account of contemporary methods of phylogenetic analysis.

In recent years, paleontologists have turned strongly toward the use of analytical methods that place their fossils in the context of biology generally, hence the increasing use of the term paleobiology. A major debate now rages dealing with the methods of interpreting fossils in systematic studies. Partly this involves the uses to which the stratigraphic information about fossils can be put. At one extreme are those who argue that the age of known fossils cannot give reliable information about the direction of evolutionary change because the fragmentary nature of the record makes it unlikely that correct temporal sequences will be preserved and discovered, and therefore that fossils should not be designated as direct ancestors of later forms. Instead, it is suggested that all forms should be treated as terminal groups in cladograms. At another extreme is the traditional paleontological habit of linking together many or all fossils, however imperfect, into ancestor-descendent sequences. The heart of the matter is the need for rigorous character analysis, recognition of specimen limitations, and an amiable consideration of other viewpoints. The continuing discovery of new and often remarkable fossil birds is intriguing, but in my opinion it is the controversy over methodology that makes paleornithology the exasperating field that it is today.—Robert J. Raikow.

Character Variation and Evolution of Sibling Species in the *Empidonax difficilis-flavescens* Complex (Aves: Tyrannidae). By Ned K. Johnson. Univ. Calif. Publ. Zool., Berkeley, California, Vol. 112, 1980:x + 151 pp., 3 black-and-white plates, 39 figs., 15 tables, 2 appendices. $9.50.—Someday in the distant future of avian systematics, every complex of geographically variable species and species-groups should be treated by a monograph such as this one, precisely describing the nature and extent of character variation throughout the ranges of its component taxa. Degrees of geographic concordance between variable characters should be analyzed, clines and discontinuities identified statistically and trinomials defended on precisely stated, objective grounds. Areas of uncertainty, and the role of human judgement, should be clearly defined whenever they appear. Behavior should be analyzed along with morphology.

This is not just an idle pipe-dream wafting out of forgotten museum corridors. Phenotypic variation is the grist upon which natural selection operates to produce genetic change and evolution. Careful analyses of patterns of variation thus represent one of the best tools we have for examining the ongoing processes of adaptation and speciation. Furthermore, birds are among the few animal groups in which such analyses are relatively easy to perform, and their rapid responses to differing selection pressures make them especially informative in this respect.

Although we still lack even a single example of a truly complete statistical evaluation of character variation, Johnson's newest contribution to the biosystematics of the genus *Empidonax* is within striking distance of the ideal model. Johnson examines patterns of variation in external morphology, color, and voice within a two-species complex distributed from British Columbia to Panama. He uses a wealth of data, and modern statistical procedures, to focus on critical questions regarding biogeographic, ecological and evolutionary implications of character variation within the superspecies. He concludes with a well-defended taxonomic treatment in which the Yellowish Flycatcher (*E. flavescens*) is recognized at the

specific level, and several confusing forms with uncertain breeding distributions are synonymized into 5 well-defined subspecies of Western Flycatcher (*E. difficilis*). His treatment was adopted in the recent volume 8 of Peters' Checklist of Birds of the World.

The data base of this monograph consists of external measurements and quantitative color indices from 1284 specimens known to have been taken on breeding grounds and sound recordings made from 208 individual flycatchers in the field. For the first time, vocal characters are analyzed with nearly the same rigor as are classical morphological characters. (However, levels of individual and contextual variation in voice are not examined carefully, thereby weakening the conclusions in some cases.) The data presentation and conclusions are based on 3 statistical procedures. Two of these—principal components and phenogram analyses—are widely used multivariate approaches for clustering populations hierarchically according to degrees of numerical similarity between them. Strictly a phenetic study, this report includes no discussion of primitive-derived sequences or directions of evolution, outside of a few generalized hypothetical scenarios near the conclusion. The advantages and drawbacks of this phenetic approach at the species, subspecies and population level of analysis are abundantly discussed elsewhere, and will not be addressed here. Johnson's stated intent was to statistically assess the nature and geography of variation within the entire complex, and to draw evolutionary inferences from the observed patterns. For the most part, his assumptions are stated or clearly implied.

The third statistical approach still is relatively little-used in ornithology, although mammalogists have begun using it extensively. Under the alliterative but uninformative term "Sum of Squares Simultaneous Test Procedure" (SS-STP), this univariate, multiple range analysis ranks populations into statistically homogeneous subsets within the total variation represented in a single character, without regard to locality. For graphical purposes, Johnson arbitrarily splits the total variation in each character into 5 equal parts, then plots each population on a map using a symbol that displays the population's position in the 5-part ranking with respect to the character being analyzed. The procedure has several advantages and disadvantages. On the one hand, it condenses onto 1 figure a tremendous amount of information regarding gross similarities between sites. A separate figure is shown for each character analyzed, and these can be compared easily by eye. Regions bearing relatively little geographic variation, zones of abrupt character change and widely separated areas of convergence or parallelism all emerge clearly. Each figure displays the statistical significance of between-site variations by its identification of homogeneous subsets. On the other hand, the procedure is not sensitive to differing degrees of character variation between localities. Much quantitative information is lost in the mapping procedure whenever a character shows pronounced divergence in any of the populations (e.g., tail length, Fig. 13). Furthermore, in all cases the maps and accompanying graphs of statistical data require long and careful scrutiny before their full meaning, and the overall picture, can be grasped. Sometimes, scrutiny reveals no statistical difference between populations that bear different symbols on the map. It is not clear how this procedure improves upon the highly informative approach used by Crowe (Ann. South African Mus. 76:43–136, 1978), Christman (Bull. Florida State Mus., Biol. Sci. 25:157–256, 1980) and others for mapping univariate character variation using isoclines. Johnson does not address in any detail the relative advantages and drawbacks of the SS-STP technique.

A variety of novel and intriguing results are presented. Perhaps the most intriguing begins with abundant evidence that zones of abrupt character change are interspersed with broad "adaptive plateaus" in which relatively little change occurs over large areas. The importance of this is magnified by the fact that the areas of sharp change are concordant between characters, including certain aspects of color and voice, as well as various physical structures. This pattern probably typifies species with localized, highly differentiated races at

upper elevation in mountainous areas (e.g., the Andes). However, Johnson's results apply to widespread, low altitude forms showing suites of character changes across relatively tiny geographic distances. The broad picture suggests to Johnson that step-wise colonization of new areas gave rise to the modern forms. Each area represents a relatively unvarying adaptive zone, but differences are pronounced between areas. He uses this as a paradigm of evolution within the genus as a whole, and cites a zone of apparently recent contact between 2 well differentiated races in northern California as a case in which divergence, especially in voice, is just short of species-level. I would have appreciated even more elaboration on why this interpretation was favored over a vicariance model, which is the major alternative to the one presented.

Among other informative conclusions, Johnson shows a possible reversal of the "Kluge-Kerfoot" phenomenon within *Empidonax*. Intrapopulational variation appears to be inversely correlated to that between populations, when polytypic *E. difficilis* was compared to the widespread and monotypic *E. hammondii*. A detailed examination of this question would be enlightening within such a remarkably homogeneous genus.

Johnson maintains that *difficilis* shows less sexual dimorphism than does its allospecies, a potentially exciting result. However, in the one character he chose to document with tables, a glaring error is revealed in the summary table (Table 2, eighth entry in right column) and the conclusion is not supported. Together with the miniscule scale of those differences he does show, this defect (the only major one I found) left me skeptical of the overall conclusion.

I was disappointed by Johnson's cursory treatment of the cause of divergence in vocal characters during allopatry, although he neatly shows that the phenomenon frequently occurs. Clearly this is an important issue in this and other tyrannid genera. Nevertheless, Johnson skirts the question in one sentence by invoking either pleiotropy between features of song and morphology, or random differences in the auditory environments between populations. In his conclusionary, "founder-by-dispersal" model for sibling-species evolution, Johnson allows vocal characters to differentiate, albeit more slowly, along exactly the same monotonic, gradual path toward full reproductive isolation as do his morphological characters. However, his vocal data do not support this; degrees of morphological and vocal differentiation are not well correlated with one another, at least when examined carefully by eye. This complicated but critical problem remains unsolved, and, in my opinion, it remains the problem in most need of detailed study with respect to *Empidonax* evolution.

In sum, this is far more than a taxonomic work. Indeed, the well-argued taxonomic summary emerges merely as a logical and convenient byproduct of a long term study whose principal intent was to make biological sense out of a variegated pattern of physical and behavioral variation in a complex taxon. As such, in ornithology at least, Johnson's work represents a new state of the art.—John W. Fitzpatrick.

Ecology and Evolution of Lek Mating Behavior in the Long-tailed Hermit Hummingbird. By F. Gary Stiles and Larry L. Wolf. Ornithological Monographs No. 27, American Ornithologists' Union, 1979:viii + 78 pp., 15 tables, 26 figs. $8.50 ($7.50 to AOU members).—This monograph presents the results of a 4-year study of lek behavior in *Phaethornis superciliosus* in primary wet forest and second growth at Finca La Selva, Costa Rica. The social systems of the hermit hummingbirds (Phaethorninae) are poorly known, although the work on 3 species in Trinidad by D. Snow and B. Snow is an outstanding exception. This deficiency is understandable, for most species are small, drab-colored, fast moving, and therefore difficult to observe in the poor light of the dense forest understory. Stiles and Wolf studied the social organization of 4 leks on which they captured and color-marked most resident individuals. They provide a detailed description of visual and vocal display behavior

(but unfortunately no sonograms) and compare it with that of other hermits. As in other studies of hermit leks few matings were seen, probably because the frequency is low, but possibly because many occur away from leks. Homosexual copulation and "false" matings with leaves were common, and an analogy is drawn between the latter and mammalian masturbation. Seasonal and daily patterning of lek activity is described in detail and correlated persuasively with the temporal availability of nectar. The characteristics of lek sites and of male territories are also documented.

The most important sections of this paper deal with foraging ecology and the dynamics of male relationships. It is here that the authors make their two most significant contributions to our understanding of lek evolution. Previous workers have argued that the evolution of avian lek behavior is linked to the abundance and spatio-temporal dispersion of food, but few lek studies have incorporated a systematic examination of the pattern of resource distribution and exploitation. The energetically optimal male strategy in many hummingbird species is to defend a food-centered territory, which females must enter for feeding and copulation. Male Long-tailed Hermits are prevented from using this strategy because other hummingbird species aggressively exclude them from most economically defensible clumps of flowers, including the larger clusters of *Heliconia pogonantha*, which is adapted for hermit pollination and is one of the main nectar sources for *P. superciliosus*. Instead, they commute from a non-food-centered lek territory to a series of regularly-patrolled, undefendable nectar sources scattered along a "trapline." Thus, interspecific competition for food appears to have been a key influence on the evolution of the mating system in this species.

Why do males congregate in leks rather than display more solitarily? The authors reject enhanced predator detection as a significant factor, arguing that such an advantage should be restricted mainly to open habitats where several lek residents can simultaneously observe approaching predators. But the advantage could be even greater in dense forest where predator detection is more difficult, although presumably a comparable reduction in individual surveillance levels to that observed in more open habitats would be impossible.

Stiles and Wolf discovered a "dominance gradient" in *P. superciliosus* leks. The most dominant males occupied stable central territories while subordinate males held less stable peripheral ones. By analogy with other lekking species it is argued that most mating probably occurs centrally, and that the proximate cues used by females in mate selection are differential male activity levels. Central males were more closely spaced and sang more than peripheral ones. The authors postulate that hermit lek systems offer females an index of male dominance (a term they use rather loosely). But while such "information" would clearly be important in an established lek system where intermale relationships affected male mating success, I am less persuaded that it could be an important selective force favoring communal over solitary display unless it also indexed performance in some vital off-lek behavior. If the authors are correct in viewing this as a major factor in lek evolution in the Long-tailed Hermit, ancestral prerequisites must have included both a potent influence of stimulus pooling on females and a shallow dominance gradient, as indeed is currently the case.

The few sexually monomorphic lekking species are vital links in developing our understanding of lek evolution, but they have been little studied. This monograph does not really elucidate the significance of monomorphism in *P. superciliosus*, but it does establish a convincing link between surprisingly high adult male annual mortality levels, the absence of sexual bimaturism, and the relative shallowness and less strictly age-graded nature of the dominance gradient compared with those of other lekking birds. Food shortage in the non-lekking season is suggested as the principal source of mortality, but one cannot help wondering about the role of predation, even though males' survivorship during the lekking season when they are most conspicuous is better than that between seasons.

This monograph is well-written and contains few typographical errors. A number of im-

portant statements and conclusions are not backed by any quantitative evidence, and statistical tests of significance are used rather sparingly. Nonetheless, this is a very valuable contribution to the avian polygamy literature. The forest-dwelling lek hummingbirds are notoriously difficult to study, and the authors are to be congratulated on the depth and range of their investigation.—ALAN LILL.

FORM AND FUNCTION IN BIRDS, VOL. 1. By A. S. King and J. McLelland (eds.). Academic Press, New York, New York, 1979:xi + 459 pp. $64.50.—The first part of a 3-volume, multiauthor treatise, this book contains 7 chapters on a diversity of topics. The intent of the series is to provide fairly lengthy and detailed accounts of the functional anatomy of birds. As nearly as I can determine the meaning of "functional anatomy" in this context, it is what used to be called physiology before the latter became indistinguishable from biochemistry. The format of this work, then, is a combination of thorough descriptive anatomy with basically nonchemical interpretations of function. The latter often includes material dealing with evolutionary, comparative and adaptational aspects of form and function. Although a disproportionate amount of experimental work is still limited to a few species, especially the domestic chicken, the book definitely lies in the realm of zoology rather than poultry science.

The first chapter is a general review of principles of avian morphology by A. S. King and D. Z. King. This provides an overview of the subject as a context for the specific topics of subsequent chapters, but it is not a superficial summary of avian anatomy. Instead, the authors chose to examine the way in which the most general specializations of birds, endothermy and flight, have influenced the various organ systems. The chapter also includes an excellent review of recent controversies in avian evolution. Rather than taking sides, King and King review the pros and cons of various theories on the reptilian ancestors of birds, and the evolution of endothermy, feathers and flight.

The remainder of the book is devoted to chapters with no particular logical relationship. The editors note that the chapter sequence was unfortunately determined by the various authors' writing schedules.

Hans-Rainer Duncker provides a review of the little-studied avian coelomic cavities. An understanding of the subdivisions of the body cavity is achieved by a study of their embryonic development, their arrangement as compared to various reptilian and mammalian groups and their functional significance, especially in relation to the respiratory system. The digestive system is discussed by John McLelland. His extensively comparative account includes the oral cavity and pharynx, esophagus, stomach, intestines, pancreas and liver. The digestive system is broadly defined here to include such feeding structures as the tongue and bill as well as the alimentary canal and its glands. There is a strong emphasis throughout on adaptive variations as related to different methods of feeding and types of food.

The urinary organs are reviewed by Oscar W. Johnson. Gross and microscopic anatomy of the kidney and associated organs is analyzed in relation to function. The renal blood supply is examined in detail, including the complex renal portal system with its capability for varying patterns of blood flow through the kidney. A. B. Gilbert's long chapter on the female genital organs includes a detailed account of the avian egg as well as the reproductive organs themselves. This account is especially dependent on the domestic fowl owing to the relative lack of comparative information. The same is true for the brief chapter on the blood cells by R. D. Hodges. In the final chapter on the autonomic system, A. R. Akester emphasizes that the neural systems regulating visceral and somatic functions are not so independent as tradition and the term "autonomic" might suggest.

A high level of scholarship and thoroughness is evident throughout this book. All of the chapters are more than adequately illustrated with line drawings and photographs. Although

the chapter topics are not always closely related, some integration is provided by a comprehensive index. This valuable work is too expensive for most individual purchasers, but institutional libraries should obtain the series.—Robert J. Raikow.

Evolution of the Vertebrates, Third Edition. By Edwin H. Colbert. John Wiley & Sons, New York, New York, 1980:510 pp., 160 line drawings. $25.00.—First published in 1955 and revised in 1969, this standard textbook of vertebrate paleontology has now been revised again to incorporate new fossil discoveries, reinterpretations and the implications of the theory of continental drift. As a relatively nontechnical survey of vertebrate history it is an excellent college-level textbook. For the purposes of this journal I will limit further comments to the book's coverage of birds. Here it is disappointing because the subject is treated so briefly, about 7 pages as compared to over 200 for the mammals. Colbert justifies this on the basis that birds have relatively little diversity, especially in the parts that fossilize; there is much truth in this. Nevertheless, there are many fascinating forms that should merit additional discussion, such as the Cretaceous toothed birds, the great flightless land birds of the early Cenozoic, the pseudo-toothed *Osteodontornis* and the extensive Pleistocene avifauna from the California tar pits. Likewise, matters of controversy such as the reptilian group ancestral to birds, the locomotor habits of *Archeopteryx* and the various theories on the origin of flight deserve more than the passing mention that they receive.—Robert J. Raikow.

The Hawaiian Goose: An Experiment in Conservation. By Janet Kear and Andrew J. Berger. Buteo Books, Vermillion, South Dakota, 1980:154 pp., 1 color plate, 24 black-and-white photographs, numerous drawings, 37 figs., 2 tables, 8 appendices. $30.00.—The Nene, or Hawaiian Goose (*Branta sandvicensis*), has become one of man's few success stories in attempting to bring back a species from the brink of extinction, and it is fitting that a monograph be done to document these efforts. This book is a historical account of the joint effort of Hawaiian and British workers to save the Hawaiian Goose, and is broken down into 3 major sections: chapters 1 and 2 give a historical background of the Nene; chapters 3 and 4 document the captive breeding efforts in Hawaii and England; and chapters 5 and 6 deal with the release program in Hawaii and prospects for the continued existence of the species.

The book starts with a historical background on Hawaii and the avifauna beginning with the discovery of the islands in 1778 by Captain Cook. I imagine that no one who purchases this book will be without Berger's Hawaiian Birdlife (University Press, Hawaii, 1972), and much of this section, including figures, seems redundant to that effort. It is not until p. 21 that the Nene is introduced, and thereafter follows a very complete historical background on the bird. The work of Baldwin (Condor 47:27–37, 1945) is heavily relied upon as a base from which to compare population declines. The authors conclude that shooting by man and the impact of introduced ground predators have probably been the major contributing factors affecting the Nene decline.

Chapter 2 deals with the morphological, behavioral and ecological background on the Nene, covering voice, size, structural adaptations, habitat, food selection and reproduction of the bird in the wild. Sonograms of the Nene are scattered throughout this chapter as are good line drawings of the trachea, skull and feet by Tim Halliday. All habitats in which Nene have been found are described, as are food items which the birds have been known to eat. The reader is sometimes confused in this section because of the authors' ambiguity in dealing with the question of food limitation. For example, on p. 43 they say: "At present, food resources at the higher altitudes where Nene are found, are not considered to be the factor

limiting their numbers," yet on p. 52 they write: ". . . and a shortage of high-protein and high-calcium food might make a second clutch unusual in the wild," and on p. 102 ". . . the introduced wild turkeys (*Meleagris gallopavo*) might be significant competitors for the berries." They also state that the "stones" (seeds) of the pukiawe are passed through the bird undigested, and this may be, but I know of no study to date which has shown this to be true. The small amount of data presented by the authors on reproduction in the wild points up the fact that very little is still known about this bird outside of information available from captive breeding. The behavioral aspects of reproduction are well covered and are supplemented by black-and-white plates depicting various threat displays.

The next 2 chapters are the meat of the book and deal with the captive rearing programs at Slimbridge, England and Pohakuloa, Hawaii. Chapter 5 is devoted to the Hawaii program and follows it from the inception in 1927 through the present. It is evident throughout this chapter that little data were made available to the authors other than summary information, because the overwhelming amount of new information contained within the book is from the Slimbridge project. The comparison of the 2 breeding programs shows some striking differences (e.g., egg weights) but is hampered by the small sample size or lack of data from the Hawaii project. Hopefully, some day all of the information from the Pohakuloa project will be published so that a complete comparison of the 2 programs can be made.

The captive rearing program at Slimbridge is very well covered in chapter 6. More often than not avicultural efforts such as this are left unpublished, and this synthesis of the Nene program at Slimbridge is the major ornithological contribution of the book. The topics of husbandry, pairing, breeding season, fertility, clutch and egg size, hatching and growth, mortality, and a comparison with the Hawaii program are made. There is a wealth of information presented in this chapter, but instead of being synthesized into a format useable to scientists, the data are presented in raw form (often percentages), and principally in appendices. Many superficial comparisons of the data are made, but the reader is often left wondering what statistical analysis was employed. This is compounded by the fact that the variances associated with much of the data are usually quite large. In some figures, lines of best fit are "eye-balled" through the data (e.g., Figs. 35 and 36), and major "trends" are discussed, which in one instance is the result of an aberrant point with a sample size of one (Fig. 35). However, the raw data are available in the book, and interested persons could pursue it if they so desired.

The sections on fertility and mortality of the Slimbridge flock are extremely well done, with the latter presenting detailed information on maladies, diseases and parasites of the Nene heretofore not recorded. Atherosclerosis was a very common cause of death in older birds, and other maladies included aspergillosis, avian tuberculosis and parasitic helminths. Although a number of the Nene in England had lesions indicative of avian pox, the virus was never isolated or positively identified. The authors initially qualified their diagnosis of this disease, but later in the book lapsed into assuming that avian pox was the pathogen (see Appendix 7 and Index).

Chapter 5 synthesizes much of what has been covered previously into the context of the release program in Hawaii. Separate sections deal with releases on state, private and National Park lands on Hawaii, and at Haleakala National Park on Maui to where the Slimbridge birds were returned. Reasons for the failures and successes of the releases are well documented. However, the problem of Nene band loss is mentioned only in the caption of Plate 5 and should have been dealt with at greater length. For a variety of reasons, band loss has been extensive in the wild Nene populations and has become a major problem in determining the success of the release programs.

The concluding chapter addresses the question of whether the over 1500 released birds have increased the breeding potential of the wild Hawaiian Goose and if the native population

will now be able to sustain itself indefinitely. The authors are well aware of the problems in attempting to answer these questions and write: "We still do not know, other than in general terms, what brought the species so low, and so cannot be sure that the hazards have been removed or are being effectively controlled." They continue: "Because of this inadequacy of information, it is impossible to be definite about the outcome of the reintroduction phase of the programme." However, their attempt to synthesize this problem into tentative, yet meaningful conclusions is admirable. They warn about the long-term effects of captivity on the genetic make-up, pathological conditions and the effects on behavior of the propagated birds. They further caution about the suitability of the habitat which will receive the reintroductions (e.g., predator levels, newly developed adverse factors), gradual settlement techniques and adequate follow-up surveys. They continually stress throughout the book the need for an intensive field study of the bird, and it can only be hoped that Nene managers in Hawaii will heed their suggestions. There is no question that the captive breeding program has saved the Nene from extinction, but when the authors expand their discussion to encompass other endangered species they recommend that only as a last resort should animals be taken into captivity, bred and released.

Overall, the book is well written and is easy to read. Outright errors are few, but some Hawaiian plant names are misspelled: "pukeawe" should be pukiawe; "mamani" should be mamane; "Mauna Silver Sword" should be Mauna Kea Silver Sword; the correct common name for *Melamprosops phaeosoma* is Po'o Uli not the "Black-faced Honeycreeper." There are 8 appendices of which numbers 1 and 8 add little to the book. The 143 references in the bibliography are as complete a list on the Nene as can be found. The 4-page index is adequate.

In summary, the authors should be commended for their job of tying together what is presently known about the Hawaiian Goose. They have not only provided a scholarly account of the bird, but have also successfully bridged the gap between aviculture and ornithology. Although the price of the book is quite high, even by today's inflated standards, those aviculturists who raise Nene, conservationists concerned with endangered species and ornithologists interested in the Hawaiian avifauna will find the book a good reference for their libraries.—Charles van Riper III.

Bird Community Dynamics in a Ponderosa Pine Forest. By Robert C. Szaro and Russell P. Balda. Cooper Ornithological Society, Studies in Avian Biology, No. 3, 1979:66 pp., 39 figs., 21 tables. $6.50.—This monograph reports on the breeding-bird populations of 5 ponderosa pine plots in northern Arizona that were subjected to a variety of modifications: clear-cutting, uniform thinning, strip-cutting, silvicultural cutting and an undisturbed control. Some of these manipulations were apparently feasible as a result of studies by others on the role of timber management in modifying stream flow and wood production. This study's purpose was "to measure and evaluate (1) the effects on the diversity, density, and behavior patterns of the breeding birds of the ponderosa pine forest of such results of habitat manipulation as differing foliage volumes, foliage patterns, and densities of trees, and (2) the standing crop biomass, consuming biomass, and existence energy requirements of the breeding birds on each plot." I believe that the study accomplishes the task of measuring these variables well, but that its success in evaluating these results is less notable. To some degree the copious production of data may have compounded the problems of interpretation; at any rate, an appropriate synthesis is never really accomplished. One is exposed to large amounts of only moderately digested data, and is presented with one example after another in the text, rather than a concise synthesis of emerging principles. The data reduction in many of the 39 figures and 21 tables is often minimal, although a wide array of statistical tools exists

for attacking such problems. As a consequence, in its present form this paper may be of interest primarily to investigators who work on the birds of ponderosa pine forests. On the other hand, the raw data are published for others to use.

Much of the analysis attempted deals with such topics as bird species diversity, evenness, foliage height diversity, plant species diversity, etc. The problems with many of the standard techniques of analyzing these topics are now well-known, and have generally been responsible for their decrease in popularity. In fact, the study found no correlation between bird species diversity and measures of vegetational complexity, and the authors themselves note that the technique was not appropriate to find systematic differences in a study such as theirs.

Enough of what this report is not. There are several interesting points that emerge from the study. One is the regional differences from ponderosa pine forests in other areas—population densities are particularly low here, even in the undisturbed study area. Between-year differences were also quite marked in some plots, but not others (replicates would have been welcomed here, even though they probably would be infeasible in a study conducted on this scale). Specific attention to regional and yearly differences and their likely bases would have focused this paper profitably and would have spoken to subjects now being recognized as important and interesting ones in their own right. In this paper one has to glean through several sections to pick up what commentary is presented on the subject.

The differences in bird populations between ponderosa pine forests and eastern coniferous forests are stressed, which the authors relate to the low representation of parulid warblers in the western coniferous forests (7–20% of the avifauna vs 50% or more in some eastern forests). The basis for this disparity is unclear, although the authors emphasize Mengel's thesis of geographical accident. However, it should be noted that the appropriate comparisons here are to eastern hard-pine forests (e.g., pitch, jack, loblolly, or longleaf pine), rather than the eastern spruce-fir forests that are renowned for their high and varied warbler densities.

Some interesting apparent replacements (pairs of species) were noted, with examples of apparent ecological release from plot to plot (e.g., Yellow-rumped [*Dendroica coronata*] vs Grace's [*D. graciae*] warblers). However, although these examples are treated as consistent with competition theory, no further attempt is made to establish whether or not a causal relationship exists.

Thus, the authors have collected a sizeable data set on the breeding birds of ponderosa pine forests, but they have missed a number of opportunities in their analysis of it. One hopes that they have planned further papers to exploit this resource.—Douglass H. Morse.

Conservation Biology: An Evolutionary-Ecological Perspective. By Michael E. Soulé and Bruce A. Wilcox (eds.). Sinauer Associates, Inc., Sunderland, Massachusetts, 1980:395 pp. $14.95.—This collection of reports is unique as a conservation book for several reasons, the most surprising of which is that most of the authors are "pure" scientists, and not applied biologists. The text is divided into 4 major sections: Ecological Principles of Conservation (4 chapters); the Consequences of Insularization (5 chapters); Captive Propagation and Conservation (5 chapters); and Exploitation and Preservation (4 chapters). In Part 1, Larry Gilbert presents a holistic approach to conservation biology, noting in particular the complex construction and interdependence of tropical food webs. This chapter will orient the student or non-ecologist to the great complexity of species diversity patterns in the tropics and their dependence on ecological succession. Gilbert notes the importance of constructing preserves so that key species (those having an important effect in food web cohesion, etc.) are included in an area that is diverse enough to contain all plants and animals important to

their continued existence. John Eisenberg compares mammal biomass in New and Old World tropical areas. He suggests that large, hard-to-observe species (e.g., leopards, jaguars) should be studied to gauge the "health" of the environment to be preserved, because they are often sensitive to environmental degradation. Jared Diamond reviews the conservation aspects of island biogeography theory as applied to patchy habitats. He notes that patchy distributions pose difficult problems for preservationists intent on saving several species distributed in this manner, because one is often confronted with the choice of either making a single large preserve, which may contain only 1 or 2 species, or many small preserves, which may contain a large number of patchily-distributed species, but may not contain large populations of associated species. Throughout this volume it is suggested that large reserves are preferable to small ones. Robin Foster continues the discussion of heterogeneous environments, noting their importance to the maintenance of species diversity.

In Part 2, Bruce Wilcox reviews the well-known ideas of species equilibria and their importance to conservation strategy. John Terborgh and Blair Winter present a short essay on species extinction, and conclude that species should be kept from becoming rare if they are to persist, which is fairly self-evident. Ian Franklin presents an interesting review of the evolutionary changes that may take place in a small population. He suggests that populations must be kept above a minimal number of breeding individuals (anywhere from 50–500) if deleterious genetic effects are to be avoided. Michael Soulé continues the discussion of the genetic aspects of conservation and emphasizes the importance of maintaining high levels of heterogeneity if fitness is to remain high. Soulé uses the wolf as an illustration of how genetic considerations might require a wolf preserve to contain anywhere from 12,000–120,000 km^2 of habitat! Daniel Goodman presents a fine discussion on the application of demographic theory to conservation problems, illustrating the importance of understanding the demography of a species before attempting long-term game management practices.

Part 3 contains papers dealing with the propagation of captive animals. The various chapters by William Conway, John Senner, Kurt Benirschke et al., and Devra Kleiman point out the complex problems that must be solved in a successful propagation program. The captive species must be extremely well-studied, biologically speaking, if one wishes to propagate it so that ecological and genetic parameters are part of the propagation program. It is also an expensive endeavor. Sheldon Campbell provides a short chapter on problems of reintroducing animals to their original habitats. I would have preferred a much more detailed discussion of this topic because earlier chapters make it clear that zoos will not be a salvation for extinction-prone species.

In the final section (Part 4), Malcolm Coe reviews the status and history of wildlife conservation in Africa, while T. C. Whitmore discusses tropical rainforest conservation. R. M. Pyle presents a brief essay on nature preserve management. The final chapter by P. R. Ehrlich will be familiar to anyone who has kept up with the popular writings of this author. I feel that Ehrlich's analysis, which may appear pessimistic to some, is actually optimistic. He concludes that conservation is not a lost cause for 2 reasons: we can delay environmental destruction and then enjoy the diversity of nature that remains for the time being; and, we can possibly reach a point where it is understood, on a world-wide basis, that continued economic and population growth are antithetical to conservation. Few could argue with the first point, but realistically, who can expect the second?

This volume, like any multiauthored work, suffers from a lack of cohesion, from repetition and from a lack of continuity of style. It is not a textbook of conservation biology, but is more involved with the ethos of conservation, and should be read by everyone interested in the problem of environmental degradation. I was impressed by a single, overriding thread connecting each chapter. We need to know a lot more about the biology of species, communities and even ecosystems if we are to manage them effectively. In many cases, theory

has outstripped our empirical understanding of nature. Yet few people are engaged in autecological studies, and funding for such research is slight. Applied biology is still looked down upon by the scientific establishment, yet each author implied a desperate need for just the kind of data that are no longer considered worthwhile or elegant.

Ehrlich likened the conservation strategy of ecologists to passengers on a plane. If we were going to fly in an airplane and the pilot began tossing out a few bolts here, a flap handle there, we would probably be apprehensive about the flight. He suggests that in nature, as in an airplane, we must save all the parts, for they form an integral whole. I will close this review by continuing the analogy. If you find yourself in a plane with an unconscious pilot, what should you do? You had better learn how to fly, and you had better learn fast. At the moment, conservationists are not sufficiently united, nor are most people sufficiently concerned, to devote any significant effort to conservation biology. The authors of this volume have tried, at least to the extent of writing a chapter, but how many of us are really willing to dedicate a significant effort to conservation biology, particularly when we are rewarded for more esoteric research? If we're going to learn how to fly that pilotless airplane, we had best get to practicing while we still have some altitude. Because when that's gone, it will be too late.—Michael A. Mares.

Allan Brooks: Artist Naturalist. By Hamilton M. Laing. Special Publication No. 3, British Columbia Provincial Museum, Victoria, British Columbia, 1979:x + 249 pp., frontispiece (portrait), 8 color plates, 117 unnumbered text figs. $10.00 (paper), $16.00 (cloth).—Allan Brooks (1869–1946) was for more than 50 years a resident of southern British Columbia (Chilliwack, Sumas, Okanagan Landing, Comox). He early sustained himself by professional collecting as well as by trapping, market hunting and fishing. He assembled an important collection of more than 9000 well-made, copiously labelled bird skins now in the Museum of Vertebrate Zoology, University of California, Berkeley.

The bare facts of his life have been recorded by his wife M. Brooks (Condor 40:12–17, 1938) and H. M. Laing (Auk 64:430–444, 1947). See also appreciations by W. L. Dawson (Condor 15:69–76, 1913) and H. Harris (Condor 48:145–153, 1946).

Born in India to Northumberland parents (his father was a well-known amateur naturalist), and self-educated, Brooks (Fellow, AOU) was a modest but respectable contributor to the faunal and systematic literature. He is best remembered, however, as the illustrator of some 20 ornithological works. With Louis Agassiz Fuertes (1874–1927), he was one of the 2 principal American workers in this area for the first third of the twentieth century.

Although his painting had devoted admirers among ornithologists, as art I have long found it seriously wanting (even allowing for his self-training, for the devastating requirements of this form of illustration, and for the generally weak landscape of bird painters to the time). His vegetation is formularized, his water tritely faked, his palette limited and endlessly repetitive, running too much to baby blues and sentimental pinks. Worse, his birds seem conventionalized, sometimes almost as though traced around generic templates. There are too many surprised-looking hawks and sway-backed passerines. There is no strength of line and no subtlety; many flying birds are grotesquely misshapen. I am afraid that these responses once led me to suppose that the author of such pictures must be of weak character, a conclusion made impossible by other evidence.

Brooks was an inveterate, if taciturn, diarist and a tireless sketcher and it is here that the present, well-illustrated little book makes its principal contributions. Extensive selections from the diaries are effectively interwoven with letters and the reminiscences of veteran naturalist Laing and other friends. The picture emerges of an extraordinarily hardy, self-sufficient, hard-headed near-loner compulsively and narrowly addicted to wild creatures, the

outdoors and the practical and sporting uses of firearms for game both large and small. His marriage at the age of 57 understandably startled his friends but seems to have been successful.

Equally revealing, and more surprising, are the many previously unpublished sketches and informal studies which, if not master drawing, clearly suffer from none of the deficiencies noted above. Compare, for example, the graceful, well-appreciated, truly falconine Peregrine on p. 137 with the pop-eyed, squab-like travesty portrayed on p. 110 of J. B. May's Hawks of North America (Natl. Assoc. of Audubon Societies, 1935). Many of these sketches are charming, economical, forceful and alive with an authenticity that cannot be faked. I note especially the Spotted Owls (pp. 78, 95), magpie (p. 97), Bobolink (p. 195), Canada Goose (p. 225), Ruffed Grouse (p. 232) and Oldsquaws (p. 236).

How does one resolve the enigma of the uncommonly great gulf between sketch and finished illustration found here? As a working hypothesis, I think that this untrained and late-blooming artist (he did not achieve wide recognition until he was past 50), a man given to quick and firm convictions yet perhaps traumatized by the requirements of "finish," fell too easily into any stereotypy that worked. Once he learned "how" to do what he needed to, he saw no need for change. He never thought seriously of himself as an artist, listing his occupation as "illustrator."

As to his strength of character, if more evidence is required, Major Allan Brooks (DSO), at the age of 49, voluntarily far in advance of the British lines in February, 1918, in 2 days of furious action personally killed at least 20 enemy soldiers with his own rifle. His personal toll of the enemy, 1914–1918, was evidently far greater. He seems almost never to have spoken of this period later.

This book is slow reading at times but it is a significant document in the history of ornithology and bird painting, as well as of British Columbia. It will appeal also to those mature citizens who remember with nostalgia the Reed bird guides and the unrestricted collecting permit.

The book needs a map. Its many typographical errors may be forgiven an author who was 96 at press time. The editors, if any, are less immune to censure but overall, the harm was slight.—Robert M. Mengel.

Hawk Lady. By Stellanie Ure. Doubleday and Co., Inc., Garden City, New York, 1980:216 pp., 14 black-and-white plates with captions. $11.95.—Hawk Lady presents anecdotal accounts of the attempts of Mrs. Ure to rehabilitate raptors. She is not a professional ornithologist, but her diary-like vignettes are "down-right" honest and serve best by warning of what not to do when caring for raptors. Overcrowding birds, housing small with large species, using chicken wire on cage walls, and risking injury from mishandling are clearly examples of what not to do.

The book is aimed at a young audience, 11–13 year olds, with much biographical material about the Ure's personal lives, particularly the children's. This approach induces the author to personify nature, a common tendency in writing for children. Personification may allow insight, provided those selected attributes of nature are accurate and repeatable. If not, natural things and events are distorted. Mrs. Ure's naming of 2 Great Horned Owls (*Bubo virginianus*) after a rather base comedian team of Cheech and Chong, and symbolizing our national bird after Shakespeare's Romeo is misleading in educating the young about birds of prey.

Although the Common Flicker (*Colaptes cafer*) was incorrectly referred to as the Red-shafted Flicker, I was pleased to find the correct common name, American Kestrel (*Falco sparverius*), being used in most instances. However, the means for determining aging of

kestrels by the amount of spotting on the breast is unconfirmed. Another minor error is found in Mrs. Ure's descriptions of a Goshawk (*Accipiter gentilis*) "stooping" to its prey. The term stoop best refers to a specialized method of attacking prey by various species of falcons. This is also true of the term tercel, which designates male individuals of the Falconidae, not males of the Accipitridae as the text indicates in its reference to "tercel Cooper's Hawks" (*A. cooperii*). On the last page, under the listing of raptors, the scientific name of the Pigeon Hawk (*F. columbarius*) was misspelled.

While I cannot recommend the purchase of the book, I applaud the Ure family, especially their children, for being concerned with injured, diseased, or stranded birds of prey. I think, however, that the book reveals that we raptor biologists should provide better guidelines than presently available for the successful rehabilitation of raptors.—THOMAS G. BALGOOYEN.

STRICTLY FOR THE CHICKENS. By Frances Hamerstrom. Iowa State University Press, Ames, Iowa, 1980:136 pp., 58 black-and-white photographs, 28 illustrations. $11.95 (hard cover).—Since the mid-1930's, Fred and Frances Hamerstrom have spent the greater part of their lives in pursuit of information about the Greater Prairie Chickens (*Tympanuchus cupido*) of Wisconsin. The efforts of the Hamerstroms to understand the lives and needs of the prairie chickens have been largely responsible for saving this species from almost certain extinction in that region. By abandoning a life of comparative luxury and ease, and as biologists daring to live in more remote areas and in unconventional ways, the Hamerstroms have perhaps attracted more than their share of memorable experiences.

Strictly for the Chickens is a collection of stories about the lives of the Hamerstroms. Yet this book could scarcely be called a biography in the traditional sense. For we are not given a detailed series of interrelated chapters neatly following in chronological order. But rather, a series of "short stories" about events and experiences, perhaps roughly in chronological order, but which leave the reader to fill in by imagination much of what might have happened throughout their lives. Each chapter presents a light-hearted behind the scenes look at many of the problems, people and events through 50 years of wildlife studies in central Wisconsin.

The topics range from the struggle to survive on graduate stipends while living in formerly abandoned farmhouses, to coping with irate and incredulous neighbours who misinterpreted and exaggerated or refused to accept the well intentioned activities of wildlife biologists. Frozen water pumps and smoking wood stoves, the problems of trapping and marking prairie chickens, graduate student life, visits by federal inspectors, having and raising children, a visit to Germany, raptor banding 'on the sly,' visiting scientists and the varied antics of some 7000 observers who came to 'help' with the work have all provided moments of tension and frustration. Yet through the understanding of Frances Hamerstrom these and other events have been brought to life with warmth and humor. In the often too serious world of science, it is indeed a pleasure to be reminded of the equally important lighter moments, which help to put life back into proper perspective.

While perhaps somewhat frustrating for lack of more information about the author's life, the stories are a charming insight into the activities of 2 very interesting people. The book is easy to read and the style compels one to continue to the end of each chapter and indeed to start into another. The text is liberally sprinkled with a great deal of prairie chicken biology and the appropriate illustrations found throughout further enhance the appeal of the book. I would highly recommend this entertaining work to anyone with a desire to mix humor and biology.—ROSS D. JAMES.

The Imperative Call: A Naturalist's Quest in Temperate and Tropical America. By Alexander F. Skutch. University Presses of Florida, Gainesville, Florida, 1979:331 pp., photographs, endpaper maps, index. $20.00.—When an individual achieves prominence in an area of scientific research, others often speculate as to how that person came to be in so enviable a circumstance. Alexander Skutch occupies such a place in the field of tropical biology; he also possesses the literary skills to satisfy our curiosity with an interesting story of his early, career-forming experiences. He shares his recollections of travels and study in a vivid, personal style that should appeal to the seasoned traveler and the tropical neophite equally.

Chronologically, The Imperative Call predates his other biographical works, A Naturalist in Costa Rica and A Bird Watcher's Adventures in Tropical America, and describes the beginnings of Skutch's fascination with nature. From sketchy recountings of his boyhood spent in rural and suburban Maryland, Skutch moves on to describe his formal university training in botany. He ably recounts his first, awesome encounter with the neotropical forest, an experience that many temperate-zone trained biologists will empathize with. He relates how a chance observation of a nesting Rufous-tailed Hummingbird (*Amazilia tzacatl*) drew this serious student of botany into his dedicated study of the behavior of birds. Throughout the book, Skutch recounts his observations of birds, places and people. Mingled with these incidents are insights into his developing philosophical point of view.

The casual narrative style, moving around one incident, forward and back in time, sometimes becomes deeply involved in details of botanical or ornithological interest. Yet, for the general reader, the details should prove no deterrent to pleasure, and for those who, like Skutch, experience the "imperative call" of nature, these are gems.—George V. N. Powell.

A Field Guide to The Birds, Fourth Edition. By Roger Tory Peterson. Houghton Mifflin Co., Boston, Massachusetts, 1980:384 pp., 136 color plates, range maps. $15.00 (cloth), $9.95 (paper).—Reviewing a Peterson Field Guide for eastern North America comes almost in the same category as reviewing The Bible, for to myriads of bird watchers this book, in its various editions, has become a veritable "holy writ" and the author at least a "major prophet." The new edition arrived in the fall of 1980 preceded by one of the most intensive selling campaigns for any recent book. Indeed, its publication was the event-of-the-year in bird books. By now there can scarcely be anyone interested in birds who has not at least examined a copy, and the sales have been so large that what is said in any review cannot influence them.

Now that the furor has subsided, perhaps we can look objectively at this edition. A new edition was long overdue since the previous one appeared in 1947. In the intervening 33 years there have been a number of changes in the world of popular bird study. For one thing, bird watching has become, to quote K. C. Parkes, "an organized cult," and the numbers of people engaged in the pastime is far greater than it was in 1947. I would hazard a guess, however, that today a smaller fraction of this total are interested in birds beyond the listing stage than was the case in the 1940's. The art of bird identification has improved markedly, so that today in the hands of some people it is a much more precise skill than it was years ago. To cite only 3 examples: the increased number of bird-banders, the recent popularity of pelagic trips and the intensive studies of the autumn raptor migration have raised birders' identification skill of the fall warblers, the seabirds and the raptors to levels not prevalent in the 1940's. Unfortunately, it would appear that Peterson has not kept up with these trends, and in most ways his identification guides are more or less the same as they were in the

1930's and 1940's when he first revolutionized this art form. For this reason, I feel that the book will be most successful in introducing the tyro to the birds, and will be less successful to the more advanced birder. Perhaps that is the main purpose of the book, and if so it should meet this objective handsomely.

The dust jacket proclaims that this edition is "Completely New" and indeed it is, except for the silhouettes on the inside covers which appear to be the same as those on the last edition. A major change is that all species are now figured in color, and the illustrations, as in other recent Peterson guides, are now more nearly portraits rather than the diagrammatic drawings of past editions. A few pictures of flight patterns of waterfowl and shorebirds are still in monocolor. The number of species on a given plate has been greatly reduced, making the pictures less crowded and somewhat larger than formerly. The textual material for each species is on the page opposite the portrait of that species, thus eliminating a minor source of irritation. But as a result of this, the amount of space devoted to each species in the text is somewhat reduced, and the convenience of having text and figure together is bought at the expense of less full descriptions and less helpful information on identification. Peterson has obviously catered to the "birder" rather than to the general ornithological community. The species are no longer listed in A.O.U. Checklist order, although this may have been deliberate since the forthcoming 1983 Checklist may give us quite a different order. The English names used are those of the recent A.B.A. Checklist, and some may be unfamiliar to those not acquainted with that list.

A welcome new feature is the inclusion of 390 range maps, which are grouped at the back of the book. These maps, which were researched by Mrs. Peterson, are large enough to show detail, and are far superior to the small maps in the principal competitor of this guide. Unfortunately, bird ranges are transitory things, subject to constant change, and in any compilation of range maps it is easy to find errors. The Petersons have shown considerable bravery in publishing these detailed maps. I counted 31 maps that had major errors in the range boundaries in the region with which I am most familiar—the southern Appalachians—and no doubt others in areas at range boundaries can find as many. This is partly the result of the shifting nature of the ranges, and partly because we locals have failed to publish some of the known changes. However, if one recognizes these deficiencies the maps should be quite useful.

The illustrations deserve the most comment. In the review copy many of the plates are far too dark, especially the sandpipers and hawks; The Red-tailed Hawk (*Buteo jamaicensis*) is as dark as any melanistic western race. A few plates are washed out and far too light, i.e., the jays on p. 209 and the cardueline finches on p. 271. I have examined several other copies and have found less variation in most, and truer colors in some. Perhaps this variation in reproduction is inevitable in a mass-produced book, but at the price charged it would appear that Houghton Mifflin Company should have been more interested in quality control.

However, the faults with the plates are not solely those of reproduction, since Peterson has not been all that careful in some of his depictions. I noted small inaccuracies in such things as soft-part colors, bill shapes, bodily proportions and other fine details. Such details were not evident on the diagrammatic sketches of earlier editions but become noticeable in the portraits of this edition. It is true however, that most of these inaccuracies will not interfere with the identification of birds at a distance, but we should not take the pictures to be definitive portraits.

A serious fault is the lack of a consistent scale on the individual plates. On the plate of spotted thrushes the large Wood Thrush (*Hylocichla mustelina*) is shown approximately the same size as the diminutive Hermit Thrush (*C. guttata*), and on another plate the chickadees are about the same size as the titmice. Body proportions are often out-of-true as when the

streamlined Scissor-tailed Flycatcher (*Muscivora forficata*) is shown to be about as chunky as a kingbird.

Perhaps the most regretable portion of the book is the continued adherence to the myth that fall warblers are confusing. Many people now know how to identify the fall warblers, not only as to species, but as to sex and age class, with ease, although in some cases this does remain difficult. But Peterson has not availed himself of this expertise, which could have been forthcoming from many people. The 2 plates of fall warblers are not really very helpful, since the colors are rather muddy and dull in my copy. However, in this edition appears for the first time the admission that some (I would say many) fall Blackpoll Warblers may have dark tarsi, contrary to what earlier editions and other guides may say. It is implied that most immature males resemble females in the fall, and while this is true for some species for others it is not. Thus, contrary to the implication of Peterson, the male Black-throated Blue (*Dendroica caerulescens*) and Cape May (*D. tigrina*) warblers look alike in both age classes. This error is not going to cause any misidentifications but it is going to mislead people, and, in particular, the neophyte bander may put a bird in the wrong age class if he relies solely on this book.

The fact that many species show considerable variation in plumage is not really recognized in this book. It is regretable that the author, who apparently had *carte blanche* from the publisher, did not take the opportunity to illustrate more of this variation. For example, the 2 oversized kingfishers (p. 187) could have been reduced to make room for a picture of the immature bird which has a single breast band which is both brown and blue. But in this connection one can only wonder what the extra unlabelled head of a male Hairy Woodpecker (*Picoides villosus*) is supposed to represent.

The harm in these admittedly minor inaccuracies and omissions comes precisely because so many people do consider a Peterson Field Guide to be the "Holy Writ." Some years ago Peterson wrote about the bird watcher who sees the bird through his binoculars, not as it really is, but as the Fuertes painting looks. Today, that tyro sees the Peterson painting, and in too many cases he is going to be misled and confused.

In summary, the book will meet its unstated purpose of teaching the tyro to identify the spring birds, particularly the males—always assuming that he doesn't have one of the copies with distorted colors. At other seasons and with some species the novice will encounter problems. Novice banders should be aware of some of the deficiencies and should not follow the age and sex criteria given therein blindly. I must admit to a great sense of disappointment in this book. I feel that the author passed up an opportunity to give us more useful information than he did. In many ways, the 1947 edition was superior to this one.—George A. Hall.

Birds of the West Coast, Vol. II. By J. F. Lansdowne. Houghton Mifflin Co., Boston, Massachusetts, 1980:167 pp., 48 color portraits, 47 pages of pencil sketches. $40.00.—Being a painter of birds, I have never missed an opportunity to view, or scrutinize, almost any depiction of a bird. About 15 years ago, on one of my first visits to the home of a friend, I was captivated by paintings displayed in his dining room. The birds, a Turkey Vulture (*Cathartes aura*), a Brown Pelican (*Pelecanus occidentalis*), a Herring Gull (*Larus argentatus*) and a Sandhill Crane (*Grus canadensis*), were exceedingly well drawn and were painted in the manner in which I saw birds—with only a hint of feather detail. Upon closer inspection I found the works of art not to be by L. A. Fuertes, but by an "unknown" bird painter by the name of J. F. Lansdowne. I was tremendously impressed by these 4 works and spent a great deal of time looking at them. In the ensuing years I was, of course, to see a great deal of work by Lansdowne, but I became disappointed in his tremendous attention to detail—

detail that could be seen if a bird were sitting on the artist's table, but detail that was not evident in wild, living birds. I don't know if Lansdowne received criticism from his friends and colleagues concerning his overly-done attention to detail, but he has slowly backed away from it and his work is again "living" and beautiful. The work in the second volume of his Birds of the West Coast includes some of his finest. The first 2 paintings, Red-necked (*Podiceps grisegena*) and Eared (*P. caspicus*) Grebes, are no less than incredible; they are also rather loosely done and have a lovely softness to them. The Great Blue Heron (*Ardea herodius*) on p. 25 is one of the finest examples of Lansdowne's amazing ability to convey different textures, be they contour feathers, plumes, large secondaries, scutes on a leg or foot, or hard, dead wood, but the picture seems cramped as a vertical and would have been better as a horizontal. My favorite works are the ones featuring three Ruddy Ducks (*Oxyura jamaicensis*) on p. 45, a soft, beautifully designed picture in which the birds are superbly executed, and a rather "un-Lansdowne" painting of a Parasitic Jaeger (*Stercorarius parasiticus*) robbing a Common Tern (*Sterna hirundo*). The latter picture shows action of a sort rarely seen in Lansdowne's work—not only is the action well-conveyed, but the execution of the picture is outstanding.

Lansdowne seems to me to occasionally have some problems with proportions. The head on the Oldsquaw (*Clangula hyemalis*) on p. 40 is too small, as is that of the Golden Eagle (*Aquila chrysaetos*) on p. 51 (and featured on the dust jacket). In general, his passerine birds are not as well done as the nonpasserines. The bills and heads on the Golden-crowned Kinglets (*Regulus satrapa*) on p. 41 are too large, and the feet on the Winter Wren (*Troglodytes troglodytes*) on p. 91 appear to belong to a dried museum specimen rather than to a living bird. On the other hand, the Brown Towhee (*Pipilo fuscus*) on p. 107 is "alive" and exquisite, and the bushtits with nest on p. 87 are equally well-done and "alive."

The book is obviously made to be looked at; it is a collection of paintings. It does, however, have a page of text that accompanies each picture. The text is a combination of anecdotes and general information about the species under discussion, and is, as it should be, merely an interesting and informative adjunct to the paintings.

The inclusion of the drawings upon which the paintings were based is good. They are, to me, sometimes "better" than the final painting. I think the looseness with which they are rendered makes them very pleasing. I am not a rapid sketcher and thus, to me, it is wonderful how Lansdowne can often capture the very being of a bird with only a few simple lines.

It is impossible to mention each of the paintings, but all are beautiful and pleasant to look at. Anyone interested in birds would want to have this latest collection of Lansdowne's work. Despite any "nit-picking" criticism that I have levied, the works are outstanding and beautiful, and reproduction is good. At $40.00 the price seems right.—John P. O'Neill.

The Avifauna of the South Farallon Islands, California. By David F. DeSante and David G. Ainley. Studies in Avian Biology No. 4, Cooper Ornithological Society, 1980:vi + 104 pp., 13 tables, 2 figs., frontispiece. $10.00.—Imagine that you direct an ornithological field station. Imagine that you have access to an island with abundant seabirds and visited by migratory birds surprising both in numbers and variety. How would you exploit these opportunities? The Directors of Point Reyes Bird Observatory (PRBO) had to answer these questions when they were granted access to South Farallon Island by the U.S. Coast Guard and the U.S. Fish and Wildlife Service in 1967. This publication summarizes that part of PRBO's first 8 years of fieldwork there, which was devoted to the obvious task of describing the avifauna. Results of prior investigations, some previously unpublished, are included along with a synopsis of PRBO's findings during the subsequent 42 months. Half of this publication is a heavily annotated checklist. A total of 346 species is reported from a flo-

ristically impoverished island less than 0.5 km² in area, and the list already has been extended! Only 15 of these species bred there while this study was conducted; 5 others have bred in earlier years.

The South Farallon Islands are now established as a site where the unexpected avian visitor is to be expected. Any treatment of such an outlandish avifauna demands great care in screening and documenting records. DeSante and Ainley clearly recognized this. Many new records are substantiated by specimens or photographs. However, details for a few species "new" to California are scanty. The mere mention of a specimen, given the chance for misidentification in even the best curated collections, is insufficient. In a very few instances, PRBO's staff released birds whose value as a specimen perhaps exceeded any potential value as a banding return. However, I recognize that this is a touchy subject for a project that depends on the contributions of amateurs. The only real alternative to collecting such birds is the "rarities committee." Many, but not all, records of extreme rarities have been reviewed by the California Bird Records Committee (see Western Birds 10:169–186, 1979 [1980 for the most recent report]). Hopefully, all such records will be so reviewed in the future. I was disturbed to see a still tentative identification included (p. 104) in a publication of this caliber, because such reports have an unfortunate tendency to become fact even if they are later rejected.

An avifauna with about 17 migrant species for every (potential) breeder is quite dynamic in composition. The list of species gives cumulative totals and peak numbers for each species broken down by season, but conveys no feeling for the day to day variations in the numbers of any, excepting those so rare that all reports are enumerated. The seabirds are treated in more detail in other publications by the staff of PRBO. Other than by its amazing variety, the landbird fauna remains obscure to me even after reading this monograph. How does the avifauna as a whole change seasonally and from year to year? What weather conditions ground migrants and what conditions allow them to leave? How do these birds fare in such an extreme environment? The reader will find no answers to such questions. It is only clear that once landbirds leave South Farallon Island, they effectively vanish. A variety of methods that convey these data concisely exist. I look forward to seeing them in future PRBO publications.

The second half of this monograph is mostly a traditional biogeographic analysis of the avifauna. I think that what this section addresses is: How does one explain the commonness or rarity of species in this avifauna? I also think it mostly misses the mark. If these patterns are just the result of random phenomena, then the question is essentially trivial and PRBO's efforts are better directed elsewhere. I share with authors the belief that these patterns are more significant. Unfortunately, the biogeographic analysis presented here only rearranges the basic data without providing additional insight as to what factors produce them. The near independence of species abundance in spring versus fall is striking, yet this observation is not further pursued. It is precisely this kind of observation, and the biogeographic affinities of the avifauna, that our hypothesis should explain. More than ever I think that explanations based on the degree of navigational error required to reach South Farallon Island ultimately will prove fruitful, and that other ecological data, such as overall species' abundance, only condition this basic hypothesis.

One might expect an avifauna with so few breeding landbirds to be poor material for an "island biogeographic" analysis. The authors' efforts are most effective and strongly substantiate some serious criticisms of prior attempts at this endeavor in other island systems. They especially emphasize the need for regular censusing and care in determining the reproductive status of birds observed.

As typical of Cooper Ornithological Society publications, the monograph is technically well produced. I would have appreciated a map of the island, although sources for that map

are cited. Misspellings are scarce. If I seem overly critical, let that be taken as a compliment to PRBO. The high quality of their publications, including this, gives one high expectations. If you have a deep interest in California's avifauna or in island biogeography, this publication is worth its price. Others should insist that their local library acquire a copy.—Paul A. DeBenedictis.

Handbook of the Birds of Europe, the Middle East, and North Africa. The Birds of the Western Palearctic. Vol. 1, Ostrich to Ducks. Vol. 2, Hawks to Bustards. Stanley Cramp, Chief Ed., K. E. L. Simmons, Assoc. Ed. Authors for Vol. 1: I. J. Ferguson-Lees, Robert Gillmor, P. A. D. Hollom, Robert Hudson, E. M. Nicholson, M. A. Ogilvie, P. J. S. Olney, K. H. Voous and Jan Wattel. Authors for Vol. 2: Robert Gillmor, P. A. D. Hollom, Robert Hudson, E. M. Nicholson, M. A. Ogilvie, P. J. S. Olney, C. S. Roselaar, K. H. Voous, D. I. M. Wallace and Jan Wattel. Artists for Vol. 1: Paul Barruel, C. J. F. Coombs, N. W. Cusa, Robert Gillmor, Peter Hayman and Sir Peter Scott. Artists for Vol. 2: C. J. F. Coombs, Peter Hayman and Ian Willis. Oxford University Press, Oxford, England. Vol. 1, 1977:722 pp., 108 color plates. $85.00. Vol. 2, 1980:695 pp., 96 color plates, $85.00. Numerous range maps, black-and-white drawings, sonagrams and diagrams in each volume.—This work is fittingly dedicated to the memory of H. F. Witherby, editor of the Handbook of British Birds (1938–1941). This indicates the magnitude of the debt that Birds of the Western Palearctic (BWP) owes to its illustrious predecessor. It also indicates that BWP is in part intended as an updated version of "Witherby." But while this would have been a worthwhile project in itself, the authors decided on the more ambitious course of treating all the birds of the Western Palearctic. I applaud this decision, because while the birds of Britain and Ireland are already very well-known, those of other countries, especially in the eastern part of the region, are not. To have drawn together so much information from so many different countries and produced a synthesised account in a single work is one of the major contributions of BWP. The language problems must have been horrendous. How many of us can read papers in Polish or Bulgarian?

The Western Palearctic, as defined here (and shown on an excellent map on the inside covers) includes the Atlantic islands down to the Cape Verdes, Northern Africa down to the central Sahara, the Middle East, including northern Saudi Arabia and Iraq but not Iran, and all of European Russia (i.e., east to the Urals). This expanded geographical scope has almost doubled the number of species covered (743+ vs 424 in Witherby). The 743 figure includes 601 breeding species, 11 "regular non-breeding migrants" and 131 accidentals that have occurred in the area since 1900. In addition, an unstated number of accidentals recorded before 1900, plus some doubtful records, are briefly treated in the text.

For sequence and scientific nomenclature the authors have followed Voous, List of Recent Holarctic Bird Species (Ibis 115:612–638, 1973; 119:223–250, 376–406, 1977). This is sensible, since Voous' list has won general acceptance. With regard to English vernacular names, however, they have evaded their responsibilities. It was the manifest duty of this new "bible" on European birds to bring needed change to these names, but as in all previous British checklists and field guides the authors have buried their heads in the sand, hoping that The Swallow would fly away. There is not a single sentence in the 36-page introduction dealing with the subject, and as we thumb through the text we meet once again our old, unmodified friends (The) Cormorant, (The) Bittern, (The) Wigeon, (The) Teal, (The) Eider, (The) Buzzard, (The) Partridge, (The) Quail and (The) Coot. We even find my old favorite, the Andalusian Hemipode, bless its little pink heart, though at least in this case someone has shamed the authors into providing an alternative name in parentheses (Little Button-Quail).

Before the species accounts there are summaries of each order and family. The orders are briefly treated, but the family summaries can run to 2 pages. They are nicely done and form

a miniature reference work by themselves. The species accounts are long and detailed. In Vol. 1, 158 species are covered in 662 pages, an average of about 4 pages per species. Accidentals receive cursory treatment while well-known birds have much lengthier accounts—the Grey Heron rates 10 pages. These are large pages (10″ × 8″) of fairly close-set type, and no space is wasted on broad margins.

The accounts are broken down into sections. Field Characters is fairly lengthy, about half a page, rather a misnomer if you are expecting a few Peterson-type italicised field marks. All plumages are described briefly, plus size, shape, notes on similar species, and habits and behavior if helpful for identification. For the ordinary birder this section is of inestimable value. The habitat section contains a complete list of habitats in different parts of the bird's range, also taking into account altitude, season, migration and other activities. As an indication of the thoroughness of this work, 5 pages of the introduction are devoted to a glossary defining the terms used in this section. Distribution for all breeding species and regular migrants is shown by 2 maps, a small scale one of the world range and a large scale one of the range in the Western Palearctic. The maps are large (large scale ones up to three-fourths of a page), and in contrasting colors, red for breeding range and gray for winter range. They are mostly easy to read, but a narrow strip of gray along a coastline can be difficult to see. In central Europe the boundaries of many small countries come close together, and it can be hard to tell if a bird occurs in, say, Switzerland or not. Regrettably, there is no text to turn to in these cases. The distribution section is short and only intended to supplement the maps with information on isolated occurrences and recent range extensions. The onus of providing distributional information thus lies entirely on the maps. While a full range description for each bird would have added to the bulk of the book, I have often been frustrated by "borderline" cases. Here is one field where Witherby still reigns supreme—its tremendous coverage of localities.

The section on population takes the place of what is usually called "status," though sometimes local status is indicated under "distribution." There is tremendous country-by-country detail of birds easily censused, like the Grey Heron (*Ardea cinerea*), but this section can be very short for birds not well-known, such as Velvet Scoter (*Melanitta fusca*). There seems to be a studious avoidance of such ill-defined terms as "common," "abundant," or "scarce" with reference to status in general, which is never clearly defined. Perhaps these terms are thought too "unprofessional" for a book like this, but it does mean one must do a lot of reading and draw inferences from population counts and distribution maps to determine if a given bird is commonly met with or not. A couple of lines giving a generalised status of each species would save a lot of eye-work. There are plenty of trees; what we want is a quick look at the forest. The section on movements includes not only regular migration but other things like dispersal, nomadism, irruptions and altitudinal migration. Under foods an exhaustive list of food items are provided and methods of feeding are also described.

Social pattern and behaviour covers such subjects as flocking, pair bonds, territoriality and roosting and deals with courtship displays, antagonistic behaviour, and other interactions. Displays are frequently illustrated by excellent drawings. Descriptions of displays and other activities are largely factual. The more difficult subject of interpretation has been avoided. A lengthy catalog of sounds, vocal and non-vocal, including calls of the young, liberally illustrated by sonagrams make up the voice section. An attempt has also been made to indicate the significance of vocal signals, in part by categorising them as, e.g., advertising calls, threat calls, alarm calls, alighting calls, greeting calls, etc. Not content with a simple catalog, the authors state that "every utterance has to be evaluated in relation to its role in behaviour, communication, and location. . . ." The lengthy (12-page) section on voice in the introduction is largely a dissertation on the problems of describing and interpreting avian vocalizations. Under breeding subjects treated include season, nest, eggs, clutch-size,

number of broods, incubation period, development of young, fledging period and breeding success. Finally, we come to a complete description of the bird, broken down into plumages, bare (not soft) parts, moults, measurements, weights and 'structure,' which includes shape, proportions, wing formulae, numbers of wing and tail feathers, etc. At the very end is a section on geographical variation. This is brief and to the point, not a lengthy discussion.

I have indicated in some detail what can be found between the covers of these volumes because that is their greatest asset—massive amounts of detailed information. One might retitle the work "Everything you've always wanted to know about European birds—but were afraid to ask." The same expansive treatment is given to the illustrations, which are present in abundance. The 743 principal species are all illustrated by color paintings said to show "every plumage which is identifiable in the field." I am sure this claim is for all practical purposes correct. The tremendous wealth of illustrations is one of the great features of this work. There are between 4 and 10 illustrations of most species, portraying breeding, non-breeding, immature, and juvenile plumages of both sexes, and downy young. Flight pictures are provided for most species; birds of prey are shown in flight from above as well as from below (a feature lacking in most field guides), and polymorphic species like Buzzards (*Buteo buteo*) and Honey Buzzards (*Pernis apivorus*) are given lavish treatment. Given the tremendous contribution made by the illustrations, I was surprised that more recognition was not given to the artists. Their names do not appear in the front of the book but are buried in the introduction. All of them deserve a great deal of credit; the plates are of very high quality.

One can find errors in any book if one looks hard enough. In this book I got no further than the Procellariiformes before I ran into trouble. Peter Hayman has done stalwart work elsewhere, but some of his seabirds are not too successful, particularly as to "jizz" or "gestalt." The flying Southern Giant Petrel (*Macronectes giganteus*) on Plate 14, with its narrow, bent and pointed wings, looks like a hybrid between that species and a Sooty Albatross (*Phoebetria* sp.). The Wandering Albatross (*Diomedea exulans*) should have a pink bill (shown here as off-white), and the text errs in referring to the bill as "appearing almost white," however likely that might seem. The bill always looks pink, even at some distance. Why are all the wanderers shown with the feet projecting beyond the tail? This is certainly not normal. The bill of an adult Black-browed Albatross (*D. melanophris*) is bright orange-yellow with a pink tip, not the washed-out brownish color shown on Plate 13. The juvenile black-brow (#8 on this plate) should have a dark bill with blackish tip, whereas it is shown with a bill like an adult. I would never have recognised the top left hand bird on Plate 16 as a Soft-plumaged Petrel (*Pterodroma mollis*), even though I have recently seen thousands of them. The shape is all wrong, and there is no hint of the dark band across the wings and rump, obvious in good light, which forms a typical *Pterodroma* 'W' pattern. The flight is described as "towering into sky." I have yet to see *mollis* tower; it flies close to the surface. The dark morph of *mollis* is stated to be "virtually indistinguishable in field from Kerguelen Petrel *P. brevirostris*." This is what I call a "museum skin remark." The Kerguelen Petrel is easily told from *mollis* and other petrels by its curious flight, long glides interspersed with a few, quick alcid-like wingbeats. It also towers, unlike *mollis*!

The above remarks are only intended to show that even a "bible" may make mistakes. By and large mistakes are few, and the work maintains a high level of excellence. Birds of the Western Palearctic is a must for every library, public or private. Even though the cost of acquiring all 7 volumes (5 more are planned) will be considerable, it is the best ornithological investment I know.—Stuart Keith.

Migrant Birds in the Neotropics: Ecology, Behavior, Distribution, and Conservation. By A. Keast and E. S. Morton (eds.). Smithsonian Institution Press, Washington,

D.C., 1980:576 pp., 30 range maps, 169 numbered text figs., 138 tables, 33 black-and-white photos. $27.50 (cloth), $15.00 (paper).—This long overdue and highly anticipated volume is the proceedings of a symposium held 27–29 October 1977. Forty papers are unequally divided into 5 sections: Conservation (2 papers), Migration of Taxonomic Groups (5 papers), Regional Studies (23 papers), Implications of Overwintering in the Tropics (8 papers), Integrations (2 papers). Although most of the papers deal with passerine birds, shorebirds and raptors are treated, as are communities as a whole. Additional review papers deal with population biology, meterological patterns, migration strategies, food supply, mixed foraging flocks and intercontinental comparisons.

This symposium is timely in view of the potential impact of widespread destruction of tropical habitats on north temperate birds wintering in tropical America. Terborgh, in his introductory paper, estimates that habitat suitable for migrants will be gone by the turn of the century. However, we know very little about the biology of the migrants once they leave their breeding grounds in the north. Where do they go? What habitats do they use? What food do they eat? Will the destruction of tropical forests lead to a decrease in temperate migrants? An earlier argument stated that moderate to heavy tropical forest destruction might be beneficial to some temperate migrants that prefer "second growth" habitats. Such thoughts, however, were laid to rest when Terborgh listed 55 species know to winter in mature tropical forests, although only a few of these were obligate forest interior users. He further states that we know of no temperate migrant species that use "fenced cattle pasture, canefield or rice paddy," yet this is what much of the forest tracts are becoming.

Regional studies suggest that the number of migrants present is inversely related to distance from the breeding grounds, i.e., Mexico has more migrants than Costa Rica, which in turn has more than Panama. As a result, ecological comparisons among sites are difficult; since factors relating to abundance, competition, food habits and behavior differ geographically no single explanation for the overall ecology of migrants in the tropics is satisfactory.

Migrants occupy a wide variety of habitats ranging from coastal dunes to lowland and highland forest. Two schools of thought exist as to why second growth sites are preferentially chosen by many migrants. Willis, Karr, Morse and others seem to support the irregularity principle, that migrants tend to use irregularly abundant resources while on the wintering grounds and choose marginal or "suboptimal" habitats avoided by residents in order to reduce intense competition for resources, presumably food. Since these habitats are suboptimal, residents will not use them when the migrants leave. The other view, presented by Schwartz and others states that these second growth habitats are not marginal, that they are "won" through competition over evolutionary time with "residents," that those habitats (niches?) are used by the migrants for up to 70% of the year and when they leave the sites are not used by residents, i.e., the residents know their place and stay there. There are problems with both views. There are no real data to support the claim that the second growth habitats are suboptimal and the fact that so many birds use them for at least half the year argues that they are not. However, if these sites are won by competition "at the expense of some tropical breeding residents" then one would expect that opportunistic residents temporarily would exploit the sites during the summer months. What is needed are more complete studies of the winter habitats used by migrants after they have left. Is it possible that researchers do not want to go into second growth sites because many of the "glamorous" tropical residents aren't there?

Unfortunately, the problem of what the migrants eat, especially with regards to what is available, is not answered by this symposium. This would seem, however, to be the fundamental question with regards to migrant ecology in the tropics, especially if adequate statements about their impact are to be made.

It should be noted that Cox's long overlooked 1968 paper on "The role of competition in

the evolution of migration" (Evolution 22:180–192, 1968) has had a rebirth in this symposium. Although his original reasoning may be subject to question, the idea is interestingly supported by several of the symposium papers. Also, one should be aware that the "south ancestral home" theory of migration evolution is apparently alive and well, in that it is supported by at least 5 of the symposium papers.

Care should be taken in interpretation of bird census data presented in this symposium. By my count at least 17 different "censusing" techniques were used in the different studies. These ranged from Johnson's casual observance of "birds seen on the walk down the road," to Russell's "regularly surveyed" plots, to Willis' "scale of censused abundance," to Pearson's species lists, to Tramer and Kemp's 6 "visual/auditory counts." Both Hilty and Hespenheide used "trail side censuses" while several walked modified Emlen transect lines or did strip censuses of varying (10, 20, 40 m) widths. The Waide, Emlen and Tramer study actually used 3 different methods on 21 sites (9 sites were censused by "counts of birds seen on repeated visits," 6 sites were censused using mist nets, 6 sites were censused using Emlen lines). The data for this paper were collected in different time periods (December–May) on different sites and yet all the data are pooled into one table with a special column labeled percent migrant individuals. So many sources of variation suggest caution in comparative interpretations such as those of Terborgh and Keast. Based on my experience in the tropics, it is even more remarkable to think that one can take walks through the forest or do trailside counts or other transect techniques and expect to accurately sample the avifauna. Given the nature of the terrain, structure of the habitat, the natural history of the birds and the limitations of the above methods it would seem impossible to detect even 25% of the existing individuals.

Except for a few minor flaws and a lot of typos, Keast and Morton have done a masterful job of editing. My only complaints with style are minor, dealing mostly with wasted space; e.g., in Smith's paper 5 pictures of hawk and vulture migrations over Panama when 2 or 3 would do, in Barlow's paper 12 full page vireo range maps when they all could have fit on 1 page and 13 poorly drawn bird illustrations in the Rappole and Warner paper (which the authors cite as excellent work in their acknowledgments section).

As far as the nuts and bolts of each individual paper are concerned most are excellent in content and superbly written. One, however, stands out like a sore thumb and I wish to make a few comments about it (which I guess is a reviewer's prerogative as well as duty). The Rappole and Warner paper proves the axiom that biggest (42 pages) is not best. The paper purports to show that individuals of 14 migrant species defend well-defined (0.2–0.5 ha) territories throughout the winter, that some territorial floaters persist in peripheral areas and that these data refute the irregularity principle. These arguments are less than convincing. Territoriality is inferred in 12 of the 14 species (Table 7). Yet 2 species showed no territorial defense, 5 had 1 observation and 3 had but 3 observations. Why are 2 species missing from the table? Although "territory" size data were only collected for Hooded Warblers (*Wilsonia citrina*) based on the territory flush technique (and 12 birds were, in fact, "mapped"), territory size data for 9 additional of the 14 species are given in Table 13. How were these data obtained? Since we have no data on the proportion of floaters to territory holders and since we have fitness data for neither, we have no way of knowing if the habit is adaptive. For example, if there were, in fact, 12 territorial Hooded Warblers and 1200 floaters and each type had 2 young per pair during the breeding season, well . . . . Not only is there an absence of hard data in the paper but much of the data given in tables refutes the text. For example, Worm-eating Warblers (*Helmitheros vermivorus*) are said to respond "vigorously to playbacks of vocalizations and displayed to, and attacked, caged conspecifics," yet only 3 each caged conspecific and playback trials are listed; one is positive and 2 are negative in both cases (Table 7). Ovenbirds (*Seiurus aurocapillus*) are listed as territorial

(Table 10), but there were no responses to playback (Table 7). Moreover, in the text "this species does not respond strongly to introduced caged intruders," yet 5 of the 7 trials (Table 7) are positive but in Table 10 the species is given a negative in the response to caged conspecifics column. For the Yellow-bellied Flycatcher (*Empidonax flaviventris*) Table 10 presents a positive in both the response to playback and response to caged individual columns yet Table 7 shows only 1 trial for each. Many other statements are made throughout this paper with little or no supportive data. Sample sizes are not given and the tables often refute the text. Often the tables are so unclear that statements made in the text cannot be supported or refuted (e.g., Table 5 does not show that "some birds remained throughout the winter on the same territory and returned there the next winter," regardless of what the authors think). In sum, the Rappole and Warner paper, while potentially of major importance, is sadly lacking in credibility.

My overall impression of this symposium is that it is timely, well thought out, generally well written and much needed. There is still much to be learned and this symposium provides a foundation of information upon which to build future research. The volume asks more questions than it answers, making it a very valuable addition to the literature. It is obvious that something must be done now to preserve the tropics or, in the words of John Terborgh, the woods in North America "just won't sound the way it used to."—ROBERT C. WHITMORE.

THE BIRDS OF HACIENDA PALO VERDE, GUANACASTE, COSTA RICA. By Paul Slud. Smithsonian Contributions to Zoology No. 292, Smithsonian Institution Press, Washington, D.C., 1980:92 pp., frontispiece, 6 figs., 33 plates, 1 table. Price not given.—According to its author, this study represents "the first comprehensive report on the avifauna of any locality in the Central American arid Pacific lowlands" and "is intended to provide a point of reference for avifaunal or environmental comparisons among comparably known localities anywhere in tropical America." In the introduction, Dr. Slud discusses the biogeographic position of NW Costa Rica, comparing viewpoints of students of various groups, and finally endorsing the existing consensus that this area represents the southern terminus of the Central American Arid Pacific biota. There follows a detailed discussion of the climate, topography, and vegetation of the Guanacaste lowlands and Palo Verde, mostly abstracted from the work of Holdridge and his collaborators. The emphasis on vegetational heterogeneity within the tropical dry forest formation raises expectations that the avifauna will be treated in comparable detail. An account of the author's 3 months' fieldwork at Palo Verde follows, including notable aspects of each of his 4 visits between 1970 and 1975, two each in wet and dry seasons.

The next section, Remarks, contains the only quantitative analysis in the book; a comparison of the numbers of species seen on different visits, and species in common between visits. The general conclusion is that one might expect to see about the same number of species, and about the same proportion of species in common, in any two 2-week periods. However, landbirds were not distinguished from waterbirds in the analysis, time spent per habitat evidently was not standardized and quantitative censuses were not attempted. Moreover, another observer without Dr. Slud's skill at field identification might well come up with quite different results. The ecological relevance of these results is thus limited at best.

The rest of the text contains an annotated list of species recorded by Dr. Slud, supplemented by the observations of P. A. Opler and a few published citations. The abundance of each species is indicated, but terms like "abundant," "common," etc. are not explicitly defined, and alternate with still more vague or subjective designations as "seen daily" and "not so scarce as expected." A general indication of habitat is given (e.g., "inside woodland," "nonforest"), but no consistent attempt is made to relate habitat choice of the birds to the

information on vegetation given in the introduction, nor is the vegetation on the "study tracts" described in detail. Species recorded in adjacent areas but not at Palo Verde are included in this general list; space and coherence would have been saved by relegating them to an appendix, since for many of them the appropriate habitat simply does not exist at Palo Verde. There is a separate "hypothetical list" of other unrecorded species that occur within 30 km of Palo Verde, but again, because the habitats of many of these species are totally absent from Palo Verde, the list does not seem particularly useful. When comparing modern-day observations with those of turn-of-the-century observers like Nutting and Carriker, some attention might have been profitably paid to the possibility that the deforestation of well over 75% of Guanacaste since their observations might have had some effect on bird distributions. Finally, data on food habits, breeding, molt, etc. are given for very few species.

The 33 plates contain black-and-white photographs of habitats (mostly) in the Palo Verde area. There is much redundance here, and of the 3 plant identifications essayed, 2 are incorrect (the "guanacaste" trees of plates 1 and 16 are saman and ceiba, respectively). In general, I lament the dearth of botanical information in the book: what fruits were eaten by birds? what flowers visited? Many plates are labeled simply "view in woodland:" however attractive, these serve little purpose without more details pointed out.

One might also question the study's comprehensiveness, as a considerable amount of information available on Palo Verde birds was evidently not consulted in its preparation. Numerous competent observers associated with the Organization for Tropical Studies have worked at Palo Verde since 1971; a detailed field checklist of Palo Verde birds based upon their observations and my own over an 8-year span has been available for a dollar from OTS for several years. More importantly, since 1976–1977 important ecological studies on Palo Verde birds have been carried out by Bio. Julio Sánchez and his team from the Costa Rican Fish and Wildlife Department. This information could have added 20–25 species to Dr. Slud's list, and affected the status of many others. Given the long delay between the author's fieldwork and publication, it is unfortunate that more effort was not devoted to keeping abreast of developments: the present report is far from an up-to-date summary of what is known of Palo Verde's avifauna.

The most appropriate audience for this book might well be the better modern birding tours, for it is they who should be most interested in which and how many species they could expect to see at Palo Verde, and about where to look for them. For the ecological ornithologist, the book should provide a useful general introduction to the area and its birds—but he or she should not expect quantitative data pertinent to current problems in avian ecology.—F. Gary Stiles.

Birds of Africa. By John Karmali. The Viking Press, New York, 1980:191 pp., 72 color plates, numerous black-and-white photographs. $25.00.—This is definitely a picture book, and by no means as comprehensive as the title suggests. As the author states in his preface, these are 72 selected portraits of East African birds, his favorites among the thousands that he has taken. They are truly portraits in the sense that the pictures were taken with a wide open lens so that the bird stands sharp and clear against the blurred background. Somewhat less than half the 87 African families of birds are represented, the great majority being among the non-passerines.

There is a foreward by Roger Tory Peterson, a preface by the author giving his philosophy of bird photography, an introduction with an outline of the zoogeography of Africa, followed by the main text and plates. Each family represented is given a chapter of its own, with a general discussion of the family as a whole, and shorter paragraphs on the biology of each species on the plates. There are numerous black-and-white photos scattered through the

book, many of which give a livelier feel for the birds than the more formal portraits. The text is neither really good nor bad, but seems to have been done freehand, like the rivers in the facing relief and vegetation maps (pp. 14 and 15). The author gives a good general picture of the African continent and of the diversity of its birds, but details, such as the subdesert coast of Upper Guinea (vegetation map), should not be accepted uncritically. Following the plates is an enjoyable section, Notes on Colour Plates, which gives the circumstances under which each plate was made, and a bibliography and index.

As bird portraits, these plates are beautiful, and the color reproduction is superb. Both the birds themselves and the backgrounds are alive and natural, a tribute to the patience and eye of the photographer and the skill of the printer. At the comparatively modest price of $25.00, these portraits are a bargain.—Melvin A. Traylor.

African Handbook of Birds: Series One. Birds of Eastern and North Eastern Africa. Second Edition. By C. W. Mackworth-Praed and C. H. B. Grant. Longman Group Ltd., London, England. In U.S.A., Longman Inc., New York, New York. Vol. 1, 1980:836 pp., 53 color plates, 6 black-and-white photo plates, many line drawings and maps. $60.00. Vol. 2, 1980:1177 pp., 43 color plates, 13 black-and-white photo plates, many line drawings and maps. $75.00.—This is an unrevised reprint of the second edition (1957) of a work first published in 1952. The only changes are the addition of political maps of Africa in 1945 and 1979 so as to permit the recognition of old place names, and of brief biographies of the authors. Volume 1 treats the non-passerines and the suboscines, volume 2 the oscines. For each species the brief text covers distinguishing characters, distribution and habits. The margins contain range maps and sometimes small sketches of the birds. The color plates are somewhat faded but should serve their intended purpose adequately. These books are intended as field guides, but with coverage of nearly 1500 species even their concise organization limits their portability. For readers elsewhere these volumes should continue to serve as a good introduction to the avifauna of the area, even though the nomenclature has not been revised.—Robert J. Raikow.

A Complete Checklist of the Birds of the World. By Richard Howard and Alick Moore. Oxford University Press, New York, New York, 1980:701 pp. $49.50.—This is a 1-volume list of the birds of the world. It is similar in format and purpose to The Complete Birds of the World by Michael Walters, also published in 1980, but appears to be a more useful work. Unlike the latter book, this one contains no natural history information, but on the other hand it has several advantages. The layout and printing are superior. Walters' book lists only species, while the present work lists subspecies as well, along with their distributions. Most important, this book contains an index to the genera and species so that it is not necessary to hunt through the text for a particular form. Each species is also provided with an English name. As in other such undertakings the classification is eclectic, being based in considerable part on the Peters Check-List plus numerous more recent research papers. This literature is cited by family in a 40 page reference list, so that the book may also serve as a good introduction to the taxonomic literature of recent years. Altogether this promises to be a useful reference work for ornithologists.—Robert J. Raikow.

Wilson Bull., 93(3), 1981, pp. 438–456

REPORT OF THE CONSERVATION COMMITTEE—1980

1980, The Year of the Coast: Birds

Thousands of kilometers of undulating coastlines rim the U.S. from Washington to Maine, the Hawaiian Islands and the Alaskan Peninsula. These are fragile environments—whether arctic, temperate, or tropical—yet man and his exploitative energies despoil coastal resources unrelentingly. Historically, man has concentrated cities, commerce and recreation on coastlines that today are immense centers of human activities. Some estimates place four of every 10 industrial facilities on the nation's coast, and the ugly sores of waste disposal are all too commonplace. Drainage schemes or landfills modify our coastal endowment. Estuaries reflect the chemical and physical abuses of their upstream sources and, beyond land's end, flows the garbage of human carelessness. Tidal ecosystems are self-maintaining only so long as man does not upset the delicate balance that has evolved over the centuries. Man may claim selected areas for his own needs as long as other tracts remain undisturbed by intrusion and pollution; but this can be accomplished only with careful long-range planning. Our coasts are choking under the pressures of their own magnetism.

In their pristine condition, our coasts harbored ecological "goods and services" beyond our current imagination. Today, the richness of their species and functions is regrettably diminished. In southern Florida alone, waterbird populations have declined from 2.5 million in 1870, to 1.5 million in 1935, to 150,000 in 1974. Although early losses can be attributed to "plume hunting," declines in the past 60 years are the result of man's destruction of feeding and nesting habitat (Soots and Landin 1978).

For many birds, coastlines are requisites for nesting and feeding; still other species seek freshwater environments for breeding but tap the rich resources of the coastline during migration and wintering periods. Freshwater birds wintering on seacoasts employ various strategies. Many use any stretch of sand, gravel, or rocky shore that harbors suitable foods. Others use restricted topographical and/or ecological situations that provide protection as well as special foods (e.g., Brant, *Branta bernicla*, and eelgrass, *Zostera marina*).

Seabirds are not without adaptability. Some feed at sea, ranging over wide areas so that patchy food resources are used where they occur. Some pioneer nesting sites on islands or coastlines, precluding endemic status. Conversely, some features of seabirds potentially limit their success in a rapidly changing world. Many have low reproductive rates with delayed maturation, or experience considerable competition for nesting sites.

Nesting sites for seabirds often are uniquely situated. Some birds use rocky cliff edges or crevices where nesting sites are limited but where the nests also are well protected from predators and man. Conversely, beach sites are more available but remain vulnerable to human disturbances. Moreover, many species have proven especially sensitive to man-made disturbances because of their specialized behavioral responses to potential predation.

Offshore, uses of seacoasts are less observable, but there birds feed on schools of fish and plankton in shoal and other areas that may be especially vulnerable to pollution and concomitant loss of basic productivity. Coastal regimes represent one of our planet's more complex energy-flow systems, and, with their continued abuse, "The coast is informing us that there is a saturation point beyond which its natural functions no longer flourish, often diminish, or simply cease" (Simon 1978). With 1980 designated as the Year of the Coast, we focus on a major component of coastal systems to illustrate the national concern for natural resources—birds of the American coastline.

Geographical Review

West Coast.—The West Coast of the United States extends approximately 2750 km from the Mexican border to the Straits of Juan de Fuca in the north. This extensive mainland and island coast includes some of the richest seabird habitats found anywhere in North America. In addition to the resources of the open sea, the western coastline is interspersed with seacliffs, beaches, bays, estuaries, tidal mud flats and saltwater marshes. Four geographic areas characterize this diverse coastal environment: southern California, San Francisco Bay, Columbia River Estuary and Puget Sound in Washington.

The seacoast of southern California supports about 158 species of birds (Corwin and Heffernan 1978). Most of these sea- and shorebirds are strongly migratory, and the largest number of individuals and species are found during the autumn and spring migrations. The most abundant species during migration is the Sooty Shearwater (*Puffinus griseus*). During autumn migration, tropical seabirds such as the Magnificent Frigatebird (*Fregata magnificens*) and the Red-billed Tropicbird (*Phaethon aethereus*) which are of infrequent occurrence so far north appear along the southern California coast. Partially responsible for these occurrences is the Davidson Current, a counter-current between the coast and the cool California Current from the north-central Pacific Ocean (Small 1974).

Along the southern California coast, the continental shelf is narrow; instead, a series of ranges and basins exists. Close to these submarine banks strong northerly winds displace the surface waters, especially during May and June. The result is an upwelling of deep, cold waters rich in nutrients and dissolved oxygen, fostering a proliferation of phytoplankton—the base of virtually all marine food-chains. The abundance of pelagic birds such as jaegers (*Stercorarius* spp.), storm-petrels (Hydrobatidae) and albatrosses (*Diomedea* spp.) is related to the surface concentrations of zooplankton, schools of surfacing anchovies and spawning squids (Small 1974).

Extending from Los Angeles to Point Conception are the eight Channel Islands. During the Pleistocene, these islands were part of an archipelago associated with the continental landmass; subsequent deformation of the earth's crust and changes in sea level separated them from the mainland (Casey 1969). Two of the islands, Anacapa and Santa Barbara Island, are parks within the Channel Islands National Monument, but most of the offshore islands are relatively inaccessible to the public. Thus, nesting and roosting seabirds such as the Xantus' Murrelet (*Endomychura hypoleuca*), Cassin's Auklet (*Ptychoramphus aleutica*) and the Brown Pelican (*Pelecanus occidentalis*), an endangered species, remain undisturbed. In 1969, nesting colonies of Brown Pelicans produced almost no young because of eggshell breakage; DDT interfered with enzyme production involved with calcium mobilization from bones to egg shells (Small 1974). A major source of contamination was discharge from a Los Angeles plant that manufactured technical DDT. After 1970, this plant's liquid wastes were put in a sanitary landfill and the oceanic input of DDT declined. When DDE contamination of the birds' major food source, anchovies, declined, hatching of pelican eggs increased significantly but productivity has remained low (Anderson et al. 1975).

Besides large offshore islands, the southern California coast is characterized by sandy beaches (75% of the coast). Furthermore, the climate south from San Francisco is Mediterranean with three months of winter rains followed by a hot, dry summer. These favorable conditions make southern California a major focus of the state's human population, and thus, of recreation and economic development. Large population centers in southern California have altered the coastal habitat considerably. For example, of the vast wetlands along the Los Angeles County coast, only 110 ha remain. Dredging and filling have been the primary causes of this habitat destruction (Corwin and Heffernan 1978).

Along these sandy beaches two species breed, the California Least Tern (*Sterna albifrons browni*) and the western race of the Snowy Plover (*Charadrius alexandrinus nivosus*). At the

turn of this century the Least Tern was an abundant colonial nester along the seacoast from the Mexican border to San Francisco Bay. However, human activities reduced this population to such a low level that, by 1966, the California Least Tern was declared an endangered species. Plovers have not declined similarly, probably because of a broader breeding range (southern Washingon to southern Baja and inland); they also nest further back from the beachfronts (Small 1974).

Prospects of large discoveries of oil and gas on the California coast are favorable, whereas the Oregon-Washington coast has the least potential for petroleum development of any region considered by the Department of Interior's accelerated leasing program (Feldmann and Hershman 1978). It was under this program that portions of the Santa Barbara Channel were leased in 1968. On 28 January 1969, a well at Union Oil's Platform A blew out. As a result, 12.3 million liters of oil coated 1710 km² of channel, 160 km of shore were contaminated and an estimated 8000 seabirds died (Dedera 1970). The risk of oil spills will only increase as more tracts are leased for development. Unfortunately, the rookeries of South Anacapa Island are especially endangered because of their proximity to shipping lanes (Corwin and Heffernan 1978).

San Francisco Bay originally consisted of 1814 km², but now only 1165 km² remain (Knight 1972). The ability of the Bay to flush its waste loads has been reduced both by filling and by the diversion of the Sacramento River to southern California, cutting the river's flow into the Bay by 50% and seriously affecting the estuarine balance between salt and fresh water. Further alteration has been caused by the estimated 3.2 billion liters of waste water entering the Bay each day (Knight 1972). The remaining portions of the San Francisco Bay consist mostly of mud flats with a few pocket beaches and marshes. Tidal salt marshes are characterized by cordgrass (*Spartina foliosa*), pickleweed (*Salicornia* spp.), saltgrass (*Disticlis spicata*) and gumplant (*Grindelia* spp.). These salt marshes are used by most migrant shorebirds such as Willets (*Catoptrophorus semipalmatus*) and Marbled Godwits (*Limosa fedoa*) as roosting areas at high tide; during ebbtide the exposed mud flats become important feeding areas (Page et al. 1979). A resident species that uses salt marshes almost exclusively is the California Clapper Rail (*Rallus longirostris obsoletus*), an endangered species. This rallid once occupied most estuarine marshes of central and northern coastal California. After 1900, a significant decrease in range and numbers resulted from habitat loss (diking, filling or conversion of salt evaporation ponds) (Gill 1979).

Forty-three km west of San Francisco Bay are the Farallon Islands. Because of commercial egging in the 19th century, these small islands were declared a wildlife refuge in 1909. The Farallon Islands today contain the largest seabird colonies in the contiguous U.S. (Small 1974). Just northwest of San Francisco is the Point Reyes Peninsula, the West Coast's only National Seashore.

In Oregon and Washington the proximity of the Coast Range to the coast limits the area available for development. Furthermore, the maritime climate along this seacoast produces rainy winters (as much as 254 cm of annual rainfall) and cool, dry summers. Despite low population densities along this coast, the harbors and coastal ocean have been subject to contamination. Waste chemicals and paper mill wastes in certain estuaries cause severe pollution locally.

Of the 14 estuary systems along the Oregon coast, the Columbia River is the largest with 6075 ha. Relatively little mixing of salt and fresh water occurs in this estuary. In fact, during summer and fall it is the largest source of fresh water along the entire West Coast of the U.S. The Columbia River is an important wintering area for waterfowl. The largest concentration of Mallards (*Anas platyrhynchos*) along the Pacific Flyway occurs in the Columbia Basin. Irrigated grain farms provide an important food resource for this large population (Bellrose 1976).

Puget Sound encompasses 647,775 ha, the largest estuary in Washington. During the

spring, Puget Sound is an important breeding area for pelagic species. Puffins (Alcidae), Rhinocerous Auklets (*Cerorhinca monocerata*) and Pigeon Guillemots (*Cepphus columba*) dig burrows in cliffs and banks near the saltwater beaches of the Sound. In the fall about 10 million ducks and 1 million geese use the Pacific Flyway. Puget Sound, with its extensive shores and shore water estuaries, mud flats and marshes, is protected from direct marine influence by the Olympic Peninsula and thus provides feeding and resting areas for these waterfowl (Feldmann and Hershman 1978).

Ports on Puget Sound are prizes for the oil industry as Alaskan petroleum resources develop. Increased tanker traffic will further increase the risk of oil spills damaging the substantial resources of the Sound. For example, Puget Sound has five National Wildlife Refuges, four of which lie along an important oil-tanker route through Rosario Straits.

East Coast.—The Atlantic coast of the United States and Canada is used heavily by a great variety of sea- and shorebirds at all seasons of the year. The sea cliffs of eastern Canada are famous for their colonies of gannets, cormorants, gulls and alcids, the marshes of the Middle Atlantic States for their wintering waterfowl, and the islands and wetlands of the Southeast for their colonies of herons, pelicans and terns, and hordes of wintering shorebirds (Fig. 1).

The Atlantic Ocean has a modifying influence on the coastal climate. In the coldest weather the immediate coast from Georgia to Maine is about 5°C warmer than a few miles inland and the frost-free period is 20–40 days longer. Mean annual temperatures range from 24°C in South Florida to 6°C in eastern Maine, and mean annual precipitation from 110 cm in Maine to 150 cm in South Florida (Visher 1954). Add to this the higher average relative humidity, the greater annual precipitation and higher percentage of sunshine (Visher 1954) and it becomes clear that this is an area of high productivity.

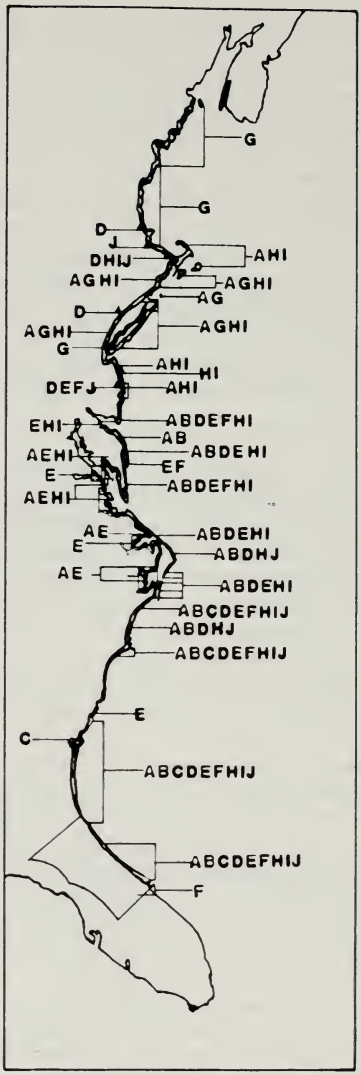
In the Mid-Atlantic Bight alone (Nantucket to Cape Hatteras), the commercial fisheries yield about 31,800 metric tons of fish and shellfish per year at a value of $70 million; and 2.5 million saltwater anglers in 1970 generated more than $318 million of business activity (Saila 1973).

As early as the colonial period the potential value of tidal marsh for agriculture and other uses was recognized, and extensive areas of tidal marsh in the Carolinas and Georgia were reclaimed for rice production (Knights and Phillips 1979). Reclamation for living space, recreation and industry has continued at an increasing pace and to these activities have been added pressures from mining, oil production, transportation, fishing, military uses, waste disposal and other direct and indirect sources of pollution that threaten the survival of not only the coastal ecosystem, but the future of our planet's living oceans. Senator Ernest F. Hollings (*in* Edge 1972), citing testimony from Jacques Cousteau, stated that life in the sea during the past 20 years had diminished as much as 30–50%.

Bird life along the Atlantic coast is rich and varied at all seasons. Saila (1973) listed 380 species from the coastal lands and offshore waters of the Mid-Atlantic Bight. Colonial nesting species have been well documented in recent years by Brown et al. (1975), Osborn and Custer (1978), Erwin (1979), Erwin and Korschgen (1979), Parnell and Soots (1979), and others.

From Massachusetts east through the Maritime Provinces, the petrels, gannets, cormorants, ducks, gulls, terns and four species of alcids nest high on rocky islands, beyond the reach of storm tides. Nevertheless, many species lead a perilous existence because of gulls and other predators and are not prepared to stand the stress of further disruption of nesting activities by human intervention.

Stretches of undisturbed beach are needed by two species of breeding plovers. Islands free of mammalian predators and human disturbances are essential for the nesting of 10 species of terns, and three of gulls (*Larus*), as well as for cormorants (*Phalacrocorax*), oystercatchers (*Haematopus*) and skimmers (*Rynchops*). Along the Middle and South Atlantic



Shorebirds : Winter Distribution

A	American Oystercatcher	G	Purple Sandpiper
B	Piping Plover	H	Dunlin
C	Wilson's Plover	I	Sanderling
D	Black-bellied Plover	J	Short-billed Dowicher
E	Willet	/	Major Winter Distribution
F	Lesser Yellowlegs	▲	Fall Migration Concentration Area

coasts many of these birds nest barely above high tide where their eggs are subject to mass destruction by storm tides; and a single visit by human intruders can also wipe out an entire year's production.

The great tidal marshes that stretch intermittently from New Jersey and Chesapeake Bay south to Florida are vital to nesting of Willets, Clapper (*Rallus longirostris*) and (locally) Black (*Laterallus jamaicensis*) rails, and Sharp-tailed (*Ammospiza caudacuta*) and Seaside (*A. maritima*) sparrows as well as to several kinds of gulls and terns. These marshes also serve as nurseries for much of the aquatic life on which the offshore fisheries depend (for humans as well as birds).

From mid-summer into mid-autumn, the coastal flats and marshes support vast hordes of migrating shorebirds en route from their Arctic nesting grounds in Canada to their winter homes in Latin America. In preparation for long non-stop flights over water, these millions of migrants require extensive unpolluted feeding grounds. For the shorebirds, waterfowl, cormorants and pelicans wintering along the Atlantic coast unpolluted coastal waters are essential. And for the gannets (*Morus*), kittiwakes (*Rissa*), fulmars (*Fulmarus*), skuas (*Catharacta*), jaegers and alcids that winter in our offshore waters, a clean environment also must be maintained.

The changing ecology of Chesapeake Bay, if not typical of trends along the Atlantic coast, may at least be symptomatic, and underscore the need for closer monitoring of habitat conditions in all coastal bays. Stevenson et al. (1979) have shown the sharp decline in submerged aquatic vegetation from 1971–1978. Using data from more than 600 sites, the percentage of stations with aquatic grasses decreased from 28–10%, and there was a comparable decrease in diversity. No single cause for this change could be proven, but contributing factors considered of minor or local importance were overgrazing by carp, cownose rays and Mute Swans (*Cygnus olor*), effects of Hurricane Agnes (in June 1972), warming trends of Bay waters, natural diseases, point-source pollutants, petrochemicals, dredging, and boat traffic. Possible major contributing factors were chlorine (about 13,200 metric tons entered the Bay in 1973), increasing levels of turbidity in shallow waters, excessive nutrients (phosphorus and nitrogen) from waste water, a dramatic increase in herbicides, and locally, competition from water chestnut (*Trapa natans*) and Eurasian watermilfoil (*Myriophyllum spicatum*).

Effects on wintering waterfowl from the loss of submerged aquatic plants have been summarized by Perry et al. (1981). Wintering waterfowl numbers have declined 50%, with only the Buffleheads (*Bucephala albeola*) showing increases. Species feeding predominantly on submerged aquatics have been affected the greatest. There has been a decline in the diversity of estuarine food organisms available and in the percentage of vegetation eaten by the ducks. Submerged aquatic vegetation is no longer a major food for Canvasbacks (*Aythya valisineria*) and Ruddy Ducks (*Oxyura jamaicensis*) wintering in Chesapeake Bay.

An example of the inadvertent loss of an endangered bird from habitat alteration in a coastal marsh is provided by the Dusky Seaside Sparrow (*Ammospiza maritima nigrescens*). Sharp (1970) contrasted the 33–34 males he found at Merritt Island, Brevard Co., Florida, in 1968, with the 70 pairs he found there in 1963, and with an indirect estimate of about 600 pairs in 1957. Annual censuses by Sykes (1980) in 1969–79 revealed 30, 18, 8, 11, 2, 2, 2, 0, 2, 0 and 0 singing males in this area. Sharp (1970) estimated a total (world) population of 894

←

FIG. 1. Winter distribution of shorebirds on the eastern U.S. coastline. Redrawn from an original map courtesy of National Oceanic and Atmospheric Administration. The Conservation Committee notes that certain winter distributions (e.g., American Oystercatcher) located north of Virginia may not be typical.

males in 1968, primarily in the St. John's River marshes. The last remnants of this population were 13 males in 1979 and 4 males and no females in 1980 (Sykes 1980). All except one male have been taken into captivity in an effort to produce a nearly pure population through backcrossing, using 2 female *nigrescens* × *peninsulae* hybrids produced in 1980 (Sykes, pers. comm.).

Causes of the final decline at Merritt Island, summarized by Sykes (1980) include elimination of about 91% of the former habitat by impounding and flooding, invasion of shrubs (and probably predators) along the dike system, and an increase in Red-winged Blackbirds (*Agelaius phoeniceus*) because of the increase in shrubs. Management activities, including dike removal and periodic burning, were undertaken in an effort to restore the habitat to its original condition, but not in time to be effective.

On the brighter side, the successful reintroduction of Common Puffins (*Fratercula arctica*) on Eastern Egg Rock in Maine (Graham 1976) demonstrates that, given sufficient knowledge, interest and support, we have the opportunity to retain important features of coastal systems.

The Gulf Coast.—Coastal habitats along the Gulf of Mexico are probably best known as wintering grounds for a large percentage of North America's waterfowl population. But in addition to providing seasonal habitat for ducks and geese, the extensive wetlands along the Gulf Coast support large migratory and resident populations of shorebirds, wading birds and other wetland species.

Climatic conditions along the Gulf Coast are somewhat varied. The growing season is long and the winter is usually mild. Summer temperatures and humidities, which are generally high, favor luxuriant vegetative growth. Precipitation is variable, but averages over 125 cm per year in all coastal areas except extreme south Texas. Rainfall is less than 80 cm per year in southern Texas and the area is semi-arid.

The southern tip of Florida is classified as a humid tropical savannah (Bailey 1978). Mangrove swamps are common in the Everglades and Florida Keys. Mangroves produce large amounts of detritus, providing the basis for food webs in the swamps. These swamps provide habitat for countless terrestrial and aquatic animals, particularly birds (Hanlon et al. 1975).

Salt and freshwater marshes are common along the upper Gulf Coast. Marshes and marsh vegetation produce large amounts of detritus that are exported from the marsh into adjacent bay waters. Kirby and Gosselink (1976) estimated 70% export of the net production from the marsh they studied; production for a Louisiana Gulf Coast salt marsh was estimated as 1176 $g/m^2/yr$. It is well documented that marshes serve as nursery grounds for commercially important fin-fishes and shellfishes. Marshes are also important habitats for migratory birds. For example, almost the entire North American population of the Lesser Snow Goose (*Anser c. caerulescens*) is dependent upon the marshes on the Louisiana and Texas coasts for winter habitat (Gosselink et al. 1974).

Barrier islands are found along many parts of the upper Gulf Coast but are most well-developed in Texas. Barrier islands have several ecological values: the dune systems protect landward areas from storm wave and tidal damage; the islands form and protect productive estuaries on the landward side; and the islands support a unique flora and fauna. In past times the barrier islands were significant nesting habitats for colonial waterbirds, especially terns and Black Skimmers (*Rynchops nigra*) (Portnoy 1977, Chapman 1980). Human encroachment has caused a drastic decline in the use of the Texas barrier islands as nesting habitat (Chapman 1980); the decline is not as drastic in Louisiana (Portnoy 1978).

In shallow bay waters at depths up to 1.5 m extensive beds of submerged seagrasses are common on the Gulf Coast. The sediments of seagrass systems perform similar functions to those of tidal marshes. Seagrass systems provide wildlife habitat and serve as spawning grounds for many marine organisms. The Laguna Madre, a 202 km long lagoon with extensive seagrass beds in southern Texas, provides rich feeding habitat for birds. In addition to large concentrations of shorebirds and wading birds, 78% of the North American population of

Redheads (*Aythya americana*) winter in the Laguna (Weller 1964). Many waterfowl use the Central Flyway, including 80% of the Pintails (*Anas acuta*), 90% of the Northern Shovelers (*A. clypeata*), 98% of the Red-breasted Mergansers (*Mergus serrator*) and 43% of the Bufleheads also winter there.

Large nesting populations of seabirds and wading birds occur along the Gulf Coast. Portnoy (1977) found 168 colonies totaling more than 847,000 breeding birds of 26 species in the coastal areas of Louisiana, Mississippi and Alabama; Chaney et al. (1978) counted more than 257,000 breeding birds of 28 species nesting along the Texas coast. Most of the colonial waterbirds in Texas nest upon dredged-material islands.

Populations of most colonial waterbird species have been declining in recent years in Texas (Chapman 1980); reliable information on population trends is not available for most of the northern Gulf Coast (Portnoy 1980). Although there are many factors that have contributed to the decline, two are probably of major importance—pesticide contamination and habitat alteration.

Before 1920, populations of Brown Pelicans were estimated at 50,000–85,000 birds in Louisiana and 5000 in Texas. The last record of nesting Brown Pelicans in Louisiana was in 1961 (Van Tets 1965) and the Texas population declined to about 100 by 1974 (King et al. 1977). Weather and disease also may have contributed to the decline of Brown Pelican populations, but there is significant evidence that pesticides contributed to the pelican decline.

Effects of habitat alteration are more difficult to assess because the changes are often subtle and may involve an alteration of the food web rather than direct avian habitat loss. For example, there is abundant nesting habitat in Texas on dredged-material islands (Chaney et al. 1978), but waterbird populations are declining as are fishery stocks in the bays. Most development of wetland habitat contributes to declining avian populations.

Hawaiian Islands.—Isolated in the Central Pacific at 19°–29°N latitude, the Hawaiian Islands span about 2400 km from the largest and most easterly island of Hawaii to the smaller Midway and Kure atolls to the west. The 10 larger Windward Islands are well known to tourists, but among the 30 or more islets, reefs and volcanic pinnacles making up the Leeward Islands are the most unique tropical seabird habitats of the U.S. Many of the Leewards were among the earliest additions to the National Refuge System in 1909.

The Hawaiian Islands are ornithologically distinctive for their many and often rare forest endemics, their evolutionary offshoots from surrounding continents and for their several species of threatened or endangered waterbirds. But the extensive and varied coastal areas serve many birds, including nesting seabirds and migratory shorebirds.

The indigenous seabirds include two albatrosses, two shearwaters, three petrels, two storm-petrels, two tropicbirds, three boobies (*Sula*), one Frigatebird (*Fregata minor palmerstoni*), six terns and noddies, and 13 other procellariiforms or pelecaniforms that are migratory visitors or stragglers. Not only do these resident birds nest on the sand and cliff shorelines, but some endemic races move inland where they nest in peaty burrows (the threatened Newell's Shearwater [*Puffinus puffinus newelli*]) or rocky burrows at elevations up to 2900 m (the endangered Dark-rumped Petrel [*Pterodroma phaeopygia sandwichensis*]). The smaller Leeward Islands are the major nesting areas for several species of seabirds that are present in tens of thousands. Best known of these are the Black-footed (*Diomedea nigripes*) and Laysan (*D. immutabilis*) albatrosses, which once nested on numerous other Pacific Islands and presumably were disturbed by human activities, just as a pioneering colony of Laysan albatrosses now is being affected on Kauai.

Five species of shorebirds regularly winter in Hawaii, and 33 have been recorded there enroute to more southerly islands and continents. However, the commonest (Golden Plover [*Pluvialis dominica fulva*]) and rarest (Bristle-thighed Curlew [*Numenius tahitiensis*]) tend to use upland areas or freshwater shorelines, respectively. Several widespread species use

the seashore, including Ruddy Turnstones (*Arenaria interpres*) and Sanderlings (*Crocethia alba*). No species of gulls are regular winter visitors, although numerous continental gulls and terns have been sighted or collected in Hawaii.

The historical use of coastal areas by birds is not well known, but there are examples suggesting that it once was much greater on the larger, now-inhabited, Windward Islands. Human disturbance has discouraged nesting in several areas in recent times, but some re-establishment has occurred. Land-use planning, pollution control and protection are particularly essential to the ecological maintenance of Hawaiian coastlines with high bird populations.

Alaska.—Because of its size and configuration, Alaska has diversity in climate and topography that influences how birds use coastal habitats. The northern Beaufort Sea coastline has severest climate in the region, with the sea being partially open only 6–10 weeks a year, and all but a few terrestrial species move south after breeding. The southeastern coast and the Aleutians have climates moderated by the sea, and although severe, they provide wintering areas for a variety of coastal seabirds and ducks supported by nutrient-rich, cold waters.

Alaska's geomorphology offers diverse coastal habitats for birds. Coastal wetlands may constitute 25–50% of the area of the Coastal Plain. Extensive lagoons formed by the dynamic shorelines and bars of the Arctic Ocean, and Izembak Lagoon of the Alaska Peninsula, harbor most of the Brant (*Branta bernicla nigricans*) of western North America during post-breeding periods and spring migration.

Huge river deltas such as the Yukon-Kuskokwim rivers of west-central Alaska and the Copper River delta of the south form extensive wetland habitats on land and enrich extensive marine areas. Both are extensively used by Brant, shorebirds and other near-shore species. Rugged cliffs of the southern coasts and many offshore islands (Pribilof, Aleutian, St. Lawrence and Kodiak islands) offer diverse nest-sites for alcids, kittiwakes, gulls and cormorants.

The southeast coast and fjordland is one of the most complex shores in North America because of the offshore islands that form a protected coastal waterway. Not only are these areas excellent for a variety of seabirds and shorebirds, but coastal fisheaters like eagles, ospreys and gulls are prominent.

The Alaskan avifauna is dominated by birds that use the coast during migration as well as breeding, and includes numerous seabirds. There are two phalaropes (Phalaropodidae), two grebes (Podicipedidae), four loons, (*Gavia*), one fulmar, three cormorants, two storm-petrels, more than 30 waterfowl, six shearwaters, two petrels, two albatrosses, three jaegers, 15 or more gulls, kittiwakes and terns, 16 alcids (including six auklets), and more than 40 shorebirds, including some Asian migrants. Large marine bays favor concentration of Southern Hemisphere shearwaters that spend the southern winter in the north. Bristol Bay is regarded as one of the greatest known concentrations of seabirds, numbering annually in the millions, and the Gulf of Alaska is a gathering area for migrants of many kinds. Offshore waters are especially important for Southern Hemisphere seabirds that migrate from the New Zealand–Australia area to the Gulf of Alaska: Slender-billed Shearwater (*Puffinus tenuirostris*) and Sooty Shearwater.

Coastal disturbance and modification, until recently, have been mostly confined to the southeastern coasts where timber, fishing and mining interests have increased activity and modified habitats. Beginning in the 1960's, exploration for, and development of, oil fields in the Cook Inlet and the Beaufort Sea have produced some pollution and habitat modifications.

Coastal Wildlife Resources.—Increasing focus on barrier islands, estuaries and sounds followed President Carter's environmental message in May 1977. In it he called for an effective plan to improve protection for Atlantic and Gulf Coast barrier islands and their associated aquatic and terrestrial habitats. Subsequent efforts produced a draft report (U.S. Dept. of the Interior 1979). It shows there are about 295 barrier islands, ranging in size from

less than 20 ha to more than 40,400 ha, from Maine to Florida and along the Gulf of Mexico to Texas. About 200 of these islands, totaling 98,400 ha, have some developments, while 95 are undeveloped. The 295 islands in 108 counties of 18 coastal states total about 648,000 ha, of which approximately 261,200 ha are managed by federal (177,600 ha), state (72,000 ha), or local (11,900 ha) governments and private conservation organizations. Of the 251,000 ha, the U.S. Fish and Wildlife Service administers 31 National Wildlife Refuges totaling 157,000 ha that contain nearly 300 km of beach in 12 coastal states from Maine to Texas. About 389,000 ha are in prviate ownership and are unprotected from future developments.

Approximately one-half of the 648,000 ha is wetland, one-quarter is barren, and one-quarter is urbanized. Because of heavy demands for development of primary and secondary home sites and recreation resorts, the barrier islands are urbanizing at a rate twice that of the nation as a whole. This unprecedented growth in wind- and water-hazardous locations is (1) exposing the owners' personal properties to high risk of damages; (2) increasing the potential for enlarging taxpayer-funded disaster relief payments; (3) usurping and continuing to threaten essential aquatic and terrestrial habitats of plants and animals; and (4) compounding pollution problems.

The estuaries and sounds protected by barrier islands from ocean winds and waves are among the most productive and richest ecosystems known. They provide nesting, resting and feeding areas for a broad spectrum of birds and mammals, as well as spawning, nursery and feeding grounds for a wide variety of fin- and shellfish. Because of their importance to the nation as natural resources and because of growing demands for housing, recreation and petroleum developments, the Office of Coastal Zone Management and the Council on Environmental Quality, jointly, have produced a data atlas on the eastern United States coastal and ocean zones (Ray et al. 1980). Each of approximately 125 maps provides information organized in five categories: (1) physical environments, 13 maps; (2) living environments, five maps; (3) distribution and status of animal and plant species, 68 maps; (4) economic activities, 29 maps; and (5) jurisdictional boundaries, and management and protected areas, 10 maps. The objective of the atlas is to identify East Coast areas least suitable for major energy and other developments, as well as areas that should be analyzed on a site-specific basis for possible special protection status because of their biological and ecological importance. Shorebird wintering areas are one example of important habitats to receive careful evaluation and consideration.

Current plans of the Office of Coastal Zone Management call for preparing similar atlases for the entire Gulf of Mexico and Beaufort, Chukchi and Bering seas off Alaska by 1982. Further information on these plans, as well as copies of the East Coast atlas, can be obtained from the Office of Ocean Resources Coordination and Assessment, Office of Coastal Zone Management, National Oceanic and Atmospheric Administration, Washington, D.C. 20235 (telephone 202/634-4120).

Environmental Perturbations

Dredging Activities.—Dredged material (= spoil) by the millions of cubic meters is removed each year in the creation and maintenance of channels in wetland habitats. Additionally, dredging is employed in the construction of harbors and marinas, in pipeline rights-of-way, and for obtaining fill or building materials (La Roe 1977).

Dredging activities and the subsequent deposition of spoil can affect adversely the coastal ecosystem in many ways. Dredging may alter water current patterns, rates of water circulation, change mixing and flushing patterns and affect salinity levels. Further, the removal, transportation and deposition of sediments often produce large quantities of silt that remain suspended in the water column; the larger sediments settle rapidly, but the finer particles may be carried great distances over extended periods of time.

Suspended silt can smother bottom-dwelling plants and animals; it can clog the gill structures of fish. High turbidities reduce vision and can mask odors, thus affecting the welfare of aquatic species. Most invertebrates, especially filter-feeders, cease feeding under a regime of high turbidity. The silt suspended during dredging operations decreases light penetration into the water, thus reducing photosynthesis and basic productivity.

Estuarine sediments, which generally have a high organic content, are aerated by the roots of marine seagrasses, but fine silts can smother plants and seal the bottom. Once this happens, the upper sediments become anaerobic and may produce toxic hydrogen sulfide deposits. The anaerobic sediments and increased biochemical oxygen demand (BOD) in the water column caused by suspended organic matter also can accentuate the reduction of dissolved oxygen in the vicinity of dredging operations.

Under normal conditions, marine seagrasses and tidal marshes are not only productive habitats for birds and other wildlife, but they also provide other benefits. These habitats prevent erosion by stabilizing emergent and submergent sediments. They also act as an efficient filtration system that maintains water quality. Removal or destruction of vegetative associations in wetlands induces instability throughout the aquatic system.

Dredging also produces material that requires disposal. Habitat is affected two ways: (1) bottom habitat is removed; and (2) the material is deposited over bottom or terrestrial habitats elsewhere. By 1967, the nation had lost 7.7% of its wetland habitat and, more recently, it was estimated that 23% of United States estuaries had been severely modified, and 50% had been moderately modified (La Roe 1977). These impacts have not been uniform as some states have experienced disproportional losses (e.g., 67% of California's estuaries have been destroyed).

Although dredging activities can have disastrous effects on wetland ecosystems, not all effects have been totally detrimental. Today more than 2000 man-made spoil islands dot the U.S. coastal and inland waterways (Soots and Landin 1978). Many of these islands have become significant breeding habitats for wildlife, most notably for colonially-nesting waterbirds. An estimated 2 million waterbirds nest on dredged-material sites, mostly along the Atlantic and Gulf coasts. As the dredged-material islands develop vegetation, they sometimes offer alternate nesting habitats similar to those found where industrial and other developments have destroyed natural systems.

In sum, however, dredging was once largely indiscriminate and without measured impacts on a wide array of wildlife and delicate ecological systems potentially affected. Cost-benefit ratios almost routinely omitted the ecological dislocations incurred when dredging was proposed, and any fortuitous outcomes (e.g., man-made islands) were random and unplanned. Only recently have systematic studies of plant succession and the related nesting requirements of seabirds been described for management purposes (Parnell et al. 1978, Soots and Landin 1978), and a useful summary of dredging impacts on birds and other wildlife was compiled by Allen and Hardy (1980).

Besides dredging, coastal environments are also vulnerable to other development or development-related activities (e.g., oil, thermal pollution, waste disposal and urbanization). From 1960–1974, U.S. offshore oil production increased from 4% of the total to 16.3% (Clark et al. 1978). Within the next 15–25 years, offshore petroleum may account for 40–50% of all domestic production. Major offshore areas include the central Gulf of Mexico, Gulf of Alaska, west Gulf of Mexico, southern California, Mid-Atlantic, east Gulf of Mexico, North Atlantic, Bristol Bay and Beaufort Sea. Effects on the onshore environment, piers, bulkheads, beach stabilization, roadways and bridges, housing, schools, recreation, etc., will be substantial (Zinn 1978).

Thermal pollution from nuclear facilities (4000 coastal nuclear parks are proposed by Weinberg and Hammond 1970) affects reproductive cycles and growth in plants and alters composition of fish communities. Effects on bird communities are relatively unknown, al-

though bird-species diversity decreased following intense thermal loading of an inland wetland in South Carolina (Gibbon and Sharitz 1974). The installed capacity of nuclear plants is expected to increase from 53 gigawatts in 1978 to 207 by the year 2000. Nineteen plants are licensed to operate on or near the coast, 15 are under construction, and 11 are planned.

Combustion of fossil fuels with high sulfur content has increased the acidity of precipitation in the northeast. A two- to five-fold increase in metric tons of sulfur oxides is projected by the year 2000 (Cavender et al. 1973). Effects include regional decreases in numbers and species in fish and invertebrate populations and a reduction in forest growth. Effects on birds again are largely unknown, but decreases in invertebrate food resources may be a factor in the survival of juvenile Black Ducks (*Anas rubripes*) in coastal marshes (J. R. Longcore, pers. comm.).

Waste disposal (industrial, agricultural and urban) is projected to affect 86% of nearly 700 coastal U.S. estuaries in 1980; most seriously affected will be the Chesapeake Bay and those along the South Atlantic Coast, Florida and the Gulf Coast (U.S. Dept. of the Interior 1970). Problems associated with components of agricultural or industrial pollution—DDT, DDE, dieldrin, polychlorinated biophenyls, kepone, lead, cadmium, mercury and others—clearly involved birds in recent decades. In sum, between 70–80% of the U.S. population will live near coastlines in the 1980's (L. Shank, pers. comm.), emphasizing the need for coastal zone management.

The Migratory Bird Treaty Act (1918) is one of four major legislative acts affecting birds and coastal management. Two cases, the U.S. vs FML, S72 F 2d 902 (2d Civ. 1978) and U.S. vs Corbin Farm Service, 444 F. Supp. S10 (E.D. Cal. 1978) affirm the protection of migratory birds from toxic pollutants, even without the intent or knowledge of the actor. Further, U.S. vs Brown, S22 F 2d 817 1977 permits Congress to enact legislation protecting federal lands from "spill over" effects of activities occurring on nearby non-federal public lands or waters.

Congress enacted the Coastal Zone Management Act of 1972 to establish a voluntary federal-state partnership for management of coastal resources. The Act encourages coastal states to participate in the development and implementation of comprehensive coastal management programs. By the end of 1979, 75% of the U.S. shoreline came under federally-approved state coastal zone management programs (Speth et al. 1979). These operate to minimize the destruction, loss, or degradation of wetlands and flood plains including those within the coastal zone. However, unsettled interpretation of the statute has lessened joint planning for coastal zones among federal and state agencies (Dedman 1979), and to date, Congress has not reauthorized federal assistance to state coastal zone management programs.

The Fish and Wildlife Coordination Act (1934) required that federal agencies give full consideration to wildlife in major water development projects. Although historically ineffective, the Act, strengthened by a presidential water policy memorandum issued in July 1978, now mandates consideration of: (1) measures to conserve wildlife, (2) alternatives to the project and (3) the implementation of conservation measures.

The fourth act is the Endangered Species Act of 1973, as reauthorized for three years in 1979. At least 27 endangered species of birds breed or have migratory areas in coastal zones (Woodard 1980). Determining critical habitat for these species, however, requires consideration of myriad economic and ecological issues.

Petroleum Discharges and Oiled Birds.—The most publicized oil spills are tanker accidents or offshore platform blowouts, but millions of tons of petroleum also enter the marine environment annually from a variety of other sources (National Academy of Sciences 1975, American Institute of Biological Sciences 1976). Approximately one-third of the total petroleum entering the sea is introduced as a result of transportation activities, of which tanker accidents comprise only a small part. River and urban run-offs account for another third of the petroleum entering marine environments. The remainder comes from coastal oil refineries, offshore production, natural seeps, atmospheric fallout and other minor sources.

Crude oil and oil products are composed of thousands of aliphatic and aromatic compounds, each possessing its own set of physio-chemical characteristics (Lee 1977). Some compounds are more toxic to aquatic organisms than others; some are more soluble than others and rapidly enter the water column and contact organisms. For example, No. 2 fuel oil, which contains toxic and soluble hydrocarbon compounds, is likely to have a greater impact on organisms than No. 6 bunker fuel, which has fewer highly toxic or soluble compounds (Nadeau 1977). Thus, the effect that an oil spill has on a marine environment is influenced by a number of factors: type of petroleum, volume spilled or released, hydrography of the affected area, climate, treatment methods, previous exposure of the affected area to petroleum releases and habitat type.

Avian mortality resulting from petroleum spills was reported as early as 1910 (Bourne 1968). It was not until 1967, however, when the Torrey Canyon accident occurred and an estimated 40,000–100,000 seabirds died, that the problem of oil-induced mortality became widely recognized (Bourne 1970). Many birds, particularly those species that spend a great deal of time in the water, are coated with oil and die from exposure when the insulative properties of their plumage is impaired. Oil also can be directly harmful when birds feed, drink, or preen; indirectly when consumed through food chains, or when applied to eggs by incubating adults. The literature dealing with toxicity of ingested oils and oiled eggs has been reviewed by Albers (1977) and Eastin (1979).

In other areas of the world, particularly in Europe and South Africa, oil pollution is believed responsible for a steady decline in seabird populations. With the current and projected demands for energy in the United States and with increased tanker traffic and accelerated development of offshore petroleum reserves, oil spills and oiled birds will become more common in our waters. In more than 100 oil spills studied throughout the world between 1960 and 1971, approximately 20% involved 50 birds or more (Ottway 1971). However, estimates of avian mortality in any oil spill may be far lower than actual mortality—deaths at sea may be 6–25 times more than the number washed ashore (Tanis and Mozer-Bruyns 1968).

Although the effects of oil on birds are the subject of much current research, few investigators have examined the results of oil spills on bird populations and their habitats. In most cases, reliable pre-impact estimates for the affected populations are scarce (Bourne 1968, Vermeer 1976), and population data on food-chains are virtually non-existent. For example, oil-contaminated sediments almost certainly have residual toxicity to invertebrate populations, and oiled hard-surfaces (e.g., rocky seashores) are not colonized easily by attaching organisms (Nadeau 1977), all potentially affecting the avian carrying capacity of an oil-impacted area.

Although the "state of the art" for cleaning oil-soaked birds has improved considerably since the Torrey Canyon disaster, birds still cannot be rehabilitated in biologically significant numbers (Williams 1977). Only a small percentage of oil-soaked birds are ever captured and brought to cleaning centers; many more that are oiled at sea never reach shore (Tanis and Mozer-Bruyns 1968, Hope-Jones et al. 1970) and still others come ashore in remote and inaccessible sites (Chapman 1981). For these reasons most recent attention has focused on deterring birds from visiting areas of oil contamination (Ward 1977).

Unfortunately, most oiled birds cannot be captured easily until they have become somewhat debilitated by oil toxicity, exposure, or starvation. Therefore, by the time that a bird reaches a treatment center, the odds for survival are already low. The success of rehabilitating an oiled bird depends upon many factors: the toxicity of the oil, the degree of plumage fouling, weather conditions to which the oiled bird is exposed, the time elapsed between oiling and treatment, the condition of the bird prior to oiling and the species involved. Of equal importance are the presence of trained personnel and the availability of appropriate equipment, supplies and facilities.

Procedures for cleaning and rehabilitation of oiled birds have been detailed by Williams

(1977, 1978). Upon capture, the initial treatment includes: (1) the removal of oil from the nostrils and mouth to prevent further oil ingestion and to permit unhampered breathing; (2) tube-feeding a warm solution of 2–5% glucose in fresh water to provide hydration and energy; (3) taping the beak shut to prevent preening and oil ingestion; (4) wrapping the bird in cloth to reduce movements and to provide insulation; and (5) putting the bird in an individual box (placed in a quiet sheltered area) for transport to a rehabilitation center.

After arrival at the center, each bird is tube-fed additional hydrating solution, weighed and banded; an oral temperature measurement is recorded. Birds with temperatures below 38°C should be held under a heat lamp producing ambient temperatures of 29–32°C. Cleaning of a bird should not commence until its body temperature approaches the normal range of 39°C.

A solvent such as Shell Solvent 70 is generally recommended for cleaning heavy viscous oils, for large birds and for cleaning large numbers of birds; detergent is recommended for small birds (Williams 1977). Care must be taken to avoid damage to feather structure. After cleaning, each bird should be dried thoroughly with hot air and kept in individual, warm pens with abundant food and water.

Cleaned birds are kept in pens until they are free from all injury and damage, capable of swimming without loss of water-proofing and are in physical condition adequate for survival in the wild. During the rehabilitation process, which may take many months, the bird must be kept free from stress. However, force-feeding is sometimes necessary during the first few days of captivity.

In most cases, mortality rates during the cleaning and rehabilitation process are high. Probably the highest success rate (41%) has been maintained by the International Bird Rescue Research Center (IBRRC, 2701 Eighth Street, Berkeley, California 94710). However, few coastal areas presently have the equipment, expertise or facilities necessary to properly clean and rehabilitate oiled birds and, as a result, most oiled birds succumb to the toxic effects of the oil, exposure or shock (Smith 1975).

Oiled-bird rehabilitation can be expensive. In the 1971 San Francisco oil spill, approximately $900 was spent per successfully released bird. During that spill 95% of the birds died in captivity. More recently, however, the IBRRC reduced costs to $15 per successfully released bird. It is not known how well rehabilitated birds survive after release. Of 218 banded birds released after treatment following the San Francisco spill, 14 were recovered dead within a few months but several were recovered up to two years later and 1046 km away (Hay 1975).

National Estuarine Sanctuary Program

The Coastal Zone Management Act of 1972, as amended in 1976, authorized a series of nationwide estuarine sanctuaries. Section 312 charged the Department of Commerce to award 50% matching grants to coastal states for their acquisition, development and operation; the sanctuaries would be owned and managed by the states.

The primary purpose of the National Estuarine Sanctuary Program is to provide long-term protection for natural areas so that they may be used for education and research. Within each sanctuary certain alterations such as dredging, filling, bulkhead construction, expansion of existing channels, creation of new channels and alteration of water circulation patterns will be prohibited. However, public use for recreation, sport and commercial fishing, hunting and wildlife observation would be permitted as long as the activities did not permanently alter the natural system or detract from its educational and research uses.

The research value of such protected areas cannot be overstated. Undisturbed estuaries permit studies of naturally-functioning systems for comparisons with disturbed areas. Clear-

ly, the protection of these sites will be invaluable for birds and other estuarine-dependent biota.

At least 20 protected estuaries were chosen to represent all geographic regions (for the purposes of the program, estuaries was defined intentionally to include the estuarine-like areas of the Great Lakes). At present, seven National Estuarine Sanctuaries are in operation. The benefits of this program will accrue to not only the coastal region where the sanctuary is located, but also to the entire nation.

Recommendations

Based on the barrier-island protection plan (Dept. of Interior 1979) and a review of statements provided by a number of conservation organizations, the following recommendations focus on actions required to maintain and improve the management of aquatic and terrestrial habitats associated with barrier islands. Individuals and organizations with a deep interest in populations and habitats of birds and other natural resources have a unique opportunity to help perpetuate these resources.

(1) Request Congress, and indeed all levels of government, to recognize fully the special ecological and biological characteristics of barrier islands and their associated habitats; and to provide a coordinated, consistent policy and appropriate planning procedures to avoid degrading, destructive and inappropriate developments. Procedures should identify means by which proposed developments can be designed to remain consistent with conservation objectives and natural resource functions and values.

The need for new ways to handle barrier islands is emphasized by a cumulative and tangled record of activities and jurisdiction; nearly 20 federal agencies have programs that impact barrier islands. One-quarter of these agencies administers programs that directly or indirectly protect barrier islands. Nonetheless, more than one-half of them administer grant, loan, permit and construction programs that have fostered adverse impacts. Another one-quarter administers property, insurance and disaster relief programs that encourage or perpetuate unwise use of these fragile, dynamic landscapes. In the past three fiscal years alone, nearly a half-billion taxpayer dollars have been committed to barrier-island developments, many of which were incompatible with the islands' physical, ecological and biological characteristics.

(2) Support the conservation concepts embodied in bills (H. R. 857 and S. 96) pending in Congress. These bills seek to establish a barrier-island protection system. The objective is to improve maintenance and management of the unique natural, ecological and biological values of barrier islands. Federal subsidies would be cut off for developing these unstable, storm-prone areas, thereby minimizing risks and threats to human life and property, while simultaneously perpetuating wild living resources—including bird populations and their habitats.

As part of its coastal barrier-island inventory, the U.S. Fish and Wildlife Service has identified in "concept plans" nearly 50 barrier islands along the Atlantic and Gulf coasts that have exceptional value for fish and wildlife. Key congressional committees handling the barrier-island bills should be urged to provide that the islands identified on the Service's list, if ultimately acquired by the federal government, be administered by the U.S. Fish and Wildlife Service as units of the National Wildlife Refuge System.

(3) Focus special attention, with research and other educational programs, on barrier islands and other coastal habitats where birds and other forms of plants and animals serve as indicators of environmental health. In particular, the National Estuarine Sanctuary sites offer functional control areas for many types of research that may act as biological cornerstones for desirable legislation and protection in the future. Pristine or near-pristine coastal environments are rarities that, with study, may stimulate the orderly recovery of already-

degraded sites elsewhere. Among the many opportunities is work dealing with densities of birds and their dependent ecological requirements in undisturbed coastal habitats. The plethora of real or potential abuses, particularly those related to petroleum extraction, suggests that ornithological activities on coastlines will be especially desirable in the coming decade.

Literature Cited

Albers, P. H. 1977. Effects of oil on birds. Pp. 61–68 *in* Proc. 1977 Oil Spill Response Workshop (P. L. Fore, ed.). U.S. Fish and Wildl. Serv., Biol. Serv. Prog., FWS/OBS/77–24.

Allen, K. O. and J. W. Hardy. 1980. Impacts of navigational dredging on fish and wildlife: a literature review. Biol. Serv. Prog., U.S. Fish and Wildl. Serv.

American Institute of Biological Sciences. 1976. Sources, effects and sinks of hydrocarbons in the aquatic environment. Washington, D.C.

Anderson, D. W., J. R. Jehl, Jr., R. W. Risebrough, L. A. Woods, Jr., L. R. DeWeese and W. G. Edgecomb. 1975. Brown Pelicans: improved reproduction off the southern California coast. Science 190:806–808.

Bailey, R. G. 1978. Ecoregions of the United States. U.S. For. Serv. Intermountain Region, Ogden, Utah.

Bellrose, F. C. 1976. Ducks, geese and swans of North America. Stackpole Books, Harrisburg, Pennsylvania.

Bourne, W. R. P. 1968. Oil pollution and bird populations. Pp. 99–121 *in* The biological effects of oil pollution on littoral communities (J. D. Carthy and D. R. Arthur, eds.). Suppl. to Field Studies Vol. 2, British Petroleum Industry, London, England.

———. 1970. Special review after the *Torrey Canyon* disaster. Ibis 112:120–125.

Brown, R. G. B., D. N. Nettleship, P. Germain, C. E. Tull and T. Davis. 1975. Atlas of eastern Canadian seabirds. Can. Wildl. Serv., Ottawa, Ontario.

Casey, H. D. 1969. The Channel Islands: their discovery. Oceans 1:69–77.

Cavender, J. H., D. S. Kircher and A. J. Hoffman. 1973. Nationwide air pollutant emission trends 1940–1970. Environmental Protection Agency, Research Triangle Park, North Carolina.

Chaney, A. H., B. R. Chapman, J. P. Karges, D. A. Nelson, R. R. Schmidt and L. C. Thebeau. 1978. Use of dredged material islands by colonial seabirds and wading birds in Texas. U.S. Army Eng. Waterways Exper. Stat. Dredged Material Res. Prog. Tech. Rept. D–78–8.

Chapman, B. R. 1980. Current status of colonial waterbird populations on the Texas coast. Pp. 14–18 *in* Management of Colonial Waterbirds (J. F. Parnell and R. F. Soots, Jr., eds.). Univ. North Carolina at Wilmington, Sea Grant Publ. UNC–SG–80–06.

———. 1981. Effects of the Ixtox I oil spill on Texas shorebird populations. Pp. 461–465 *in* Proc. of the 1981 Oil Spill Conf. Am. Petrol. Inst., Washington, D.C.

Clark, J., J. Zinn and C. Tenel. 1978. Environmental planning for offshore oil and gas. U.S. Fish and Wildl. Serv. FWS/OBS–77/12.

Corwin, R. and P. H. Heffernan. 1978. Environmental planning for offshore oil and gas. Vol. V. Regional Status Repts., Pt. 4, California. The Conservation Foundation, Washington, D.C., U.S. Fish and Wildl. Serv. Biol. Serv. Prog., FWS/OBS–77/16.4.

Dedera, D. 1970. Santa Barbara and beyond. Oceans 3:17–32.

Dedman, J. 1979. State-federal relations in the coastal zone. Pp. 175–184 *in* Proc. of Gulf of Mexico Coastal Ecosystem Workshop (L. Fore and R. D. Peterson, eds.). U.S. Fish and Wildl. Serv.

Eastin, W. C., Jr. 1979. Methods used at Patuxent Wildlife Research Center to study the

effects of oil on birds. Pp. 60–66 *in* Proc. 1979 U.S. Fish and Wildl. Serv. Pollution Response Workshop, St. Petersburg, Florida. Washington, D.C.

EDGE, B. L. 1972. Coastal zone pollution management. Clemson Univ., Clemson, South Carolina.

ERWIN, R. M. 1979. Coastal waterbird colonies: Cape Elizabeth, Maine to Virginia. U.S. Fish and Wildl. Serv., Biol. Serv. Prog., FWS/OBS–79/10.

——— AND C. E. KORSCHGEN. 1979. Coastal waterbird colonies: Maine to Virginia, 1977. An atlas showing colony locations and species composition. U.S. Fish and Wildl. Serv., Biol. Serv. Prog., FWS/OBS–79/08.

FELDMANN, J. H. AND J. J. HERSHMAN. 1978. Environmental planning for offshore oil and gas. Vol. V, Regional Status Repts., Pt. 5, Alaska, Washington and Oregon. The Conservation Foundation, Washington, D.C., U.S. Fish and Wildl. Serv., Biol. Serv. Prog., FWS/OBS–77/16.5.

GIBBON, J. W. AND R. R. SHARITZ. 1974. Thermal alteration of aquatic ecosystems. Am. Sci. 62:660–670.

GILL, R., JR. 1979. Status and distribution of the California Clapper Rail (*Rallus longirostris obsoletus*). Calif. Fish and Game 65:36–49.

GOSSELINK, J. G., E. P. ODUM AND R. M. POPE. 1974. The value of the tidal marsh. Center for Wetlands Resources, Louisiana State Univ., Publ. LSU–SG–74–03, Baton Rouge, Louisiana.

GRAHAM, F., JR. 1976. Seabirds under seige. Audubon 78(6):52–73.

HANLON, R., F. BAYER AND G. VOSS. 1975. Guide to the mangroves, buttonwood, and poisonous shoreline trees of Florida, the Gulf of Mexico, and the Caribbean Region. Univ. Miami, Sea Grant Prog. Field Guide Ser. 3:1–29.

HAY, K. G. 1975. The status of oiled wildlife: research and planning. Pp. 249–253 *in* Proc. 1975 Conf. on Prevention and Control of Oil Spills. Am. Petrol. Inst., Washington, D.C.

HOPE-JONES, P., G. HOWELLS, E. I. S. REES AND J. WILSON. 1970. Effect of the "Hamilton trader" oil on birds in the Irish Sea in May 1969. Br. Birds 63:97–110.

KING, K. A., E. L. FLICKINGER AND H. H. HILDEBRAND. 1977. The decline of Brown Pelicans on the Louisiana and Texas Gulf Coast. Southwest Nat. 21:417–431.

KIRBY, C. J. AND J. G. GOSSELINK. 1976. Primary production in a Louisiana Gulf Coast *Spartina alterniflora* marsh. Ecology 57:1052–1059.

KNIGHT, G. 1972. The Bay: San Francisco Bay and the emerging regional reality. Oceans 5:25–32.

KNIGHTS, B. AND A. J. PHILLIPS. (eds.). 1979. Estuarine and coastal land reclamation and water storage. Saxon House, Farnborough, Hants, England.

LAROE, E. T. 1977. Dredging—ecological impacts *in* Coastal ecosystem management (J. R. Clark, ed.). John Wiley and Sons, New York, New York.

LEE, R. F. 1977. Fate of oil in the sea. Pp. 43–54 *in* Proc. 1977 Oil Spill Response Workshop (P. L. Fore, ed.). U.S. Fish and Wildl. Serv., Biol. Serv. Prog., FWS/OBS/77–24.

NADEAU, R. J. 1977. Assessing the biological impact of oil spills: a new role for EPA biologists. Pp. 55–60 *in* Proc. 1977 Oil Spill Response Workshop (P. L. Fore, ed.). U.S. Fish and Wildl. Serv., Biol. Serv. Prog., FWS/OBS/77–24.

NATIONAL ACADEMY OF SCIENCES. 1975. Petroleum in the marine environment. Washington, D.C.

OSBORN, R. G. AND T. W. CUSTER. 1978. Herons and their allies: atlas of Atlantic coast colonies, 1975 and 1976. U.S. Fish and Wild. Serv., Biol. Serv. Prog., FWS/OBS/77–08.

OTTWAY, S. M. 1971. A review of world oil spillages, 1960–1971. Oil Pollution Res. Unit. Orielton Field Centre, Pembroke, Wales.

Page, G. W., L. E. Stenzel and C. M. Wolfe. 1979. Aspects of the occurrence of shorebirds on a central California estuary. Pp. 15–32 *in* Shorebirds in marine environments (F. A. Pitelka, ed.). Studies in Avian Biology No. 2. Cooper Ornithol. Soc.

Parnell, J. F., D. M. DuMond and R. N. Needham. 1978. A comparison of plant succession and bird utilization of diked and undiked dredged material islands in North Carolina estuaries. Univ. North Carolina at Wilmington, U.S. Army Eng. Waterways Exper. Stat., Tech. Rept. D–78–9.

——— and R. F. Soots, Jr. 1979. Atlas of colonial waterbirds of North Carolina estuaries. UNC Sea Grant 78–10. Raleigh, North Carolina.

Perry, M. C., R. E. Munro and G. M. Haramis. 1981. Twenty-five year trends in Chesapeake Bay diving duck populations. Proc. 46th N. Am. Wildl. and Nat. Res. Conf. In press.

Portnoy, J. W. 1977. Nesting colonies of seabirds and wading birds, coastal Louisiana, Mississippi, and Alabama. U.S. Fish and Wildl. Serv., Biol. Serv. Prog., FWS/OBS–77/07.

———. 1978. Black Skimmer abundance on the Louisiana–Mississippi–Alabama coast. Wilson Bull. 90:438–442.

———. 1980. Status of colonial waterbird populations of the Louisiana, Mississippi and Alabama coasts. Pp. 10–13 *in* Management of colonial waterbirds (J. F. Parnell and R. F. Soots, Jr., eds.). Univ. North Carolina at Wilmington, Sea Grant Publ. UNC–SG–80–06.

Ray, G. C., J. A. Dobbin, C. H. Ehler and B. J. Basta. 1980. Eastern United States coastal and ocean zones: data atlas. Off. Coastal Zone Manage., U.S. Dept. Commerce, Washington, D.C.

Saila, S. B. 1973. Coastal and offshore environmental inventory, Cape Hatteras to Nantucket Shoals. Marine Publ. Ser. No. 2, Univ. Rhode Island, Kingston.

Sharp, B. 1970. A population estimate of the Dusky Seaside Sparrow. Wilson Bull. 82:158–166.

Simon, A. W. 1978. The thin edge: coast and man in crisis. Harper & Row, New York, New York.

Small, A. 1974. The birds of California. Winchester Press, New York, New York.

Smith, D. C. 1975. Rehabilitating oiled aquatic birds. Pp. 241–247 *in* Proc. 1975 Conf. on Prevention and Control of Oil Spills. Am. Petrol. Inst., Washington, D.C.

Soots, R. F., Jr. and M. C. Landin. 1978. Development and management of avian habitat on dredged material islands. U.S. Army Eng. Waterways Exper. Stat., Tech. Rept. DS–78–18.

Speth, G., J. Yarn and R. Harris. 1979. Environmental quality. Tenth Ann. Rept. Council on Environmental Quality, GPO, Washington, D.C.

Stevenson, J. C., N. Confer and C. B. Pieper. 1979. Decline of submerged aquatic plants in Chesapeake Bay, U.S. Fish and Wildl. Serv., Biol. Serv. Prog., FWS/OBS–79/24.

Sykes, P. W., Jr. 1980. Decline and disappearance of the Dusky Seaside Sparrow from Merritt Island, Florida. Am. Birds 34:728–737.

Tanis, J. J. C. and M.F. Mozer-Bruyns. 1968. The impact of oil pollution on seabirds in Europe. Pp. 69–74 *in* Proc. Inter. Conf. on Oil Pollution of the Sea, Rome, Italy.

U.S. Department of the Interior. 1970. National estuary study. U.S. Fish and Wildl. Serv.

———. 1979. Alternative policies for protecting barrier islands along the Atlantic and Gulf coasts of the United States and draft environmental statement. Heritage Conserv. and Rec. Serv., Washington, D.C.

Van Tets, G. F. 1965. A comparative study of some social communication patterns in the Pelecaniformes. Ornithol. Monogr. 2:1–88.

Vermeer, K. 1976. Colonial auks and eiders as potential indicators of oil pollution. Mar. Poll. Bull. 7:165–167.

Visher, S. S. 1954. Climatic atlas of the United States. Harvard Univ. Press, Cambridge, Massachusetts.

Ward, J. G. 1977. Techniques for dispersing birds from oil spill areas. Pp. 113–124 *in* Proc. 1977 Oil Spill Response Workshop (P. L. Fore, ed.). U.S. Fish and Wildl. Serv., Biol. Serv. Prog., FWS/OBS/77–24.

Weller, M. W. 1964. Distribution and migration of the Redhead. J. Wildl. Manage. 28:64–103.

Weinberg, A. M. and R. P. Hammond. 1970. Limit to the use of energy. Am. Sci. 58:412–418.

Williams, A. S. 1977. Current methods of oiled bird rehabilitation, Pp. 125–134 *in* Proc. 1977 Oil Spill Response Workshop (P. L. Fore, ed.). U.S. Fish and Wildl. Serv., Biol. Serv. Prog., FWS/OBS/77–24.

———. 1978. Saving oiled seabirds: a manual for cleaning and rehabilitating oiled waterfowl. Am. Petrol. Inst., Washington, D.C.

Woodard, D. W. 1980. Selected vertebrate endangered species of the seacoast of the United States. U.S.D.I., Fish and Wildl. Serv., Washington, D.C.

Zinn, J. 1978. Environmental planning for offshore oil and gas, Vol. 2. Effects on coastal communities. U.S.D.I., Fish and Wildl. Serv., FWS/OBS–77–13.

Eric G. Bolen, *Chairman*
Brian R. Chapman
Marcia M. Wilson
Milton W. Weller
Laurence R. Jahn
Chandler S. Robbins
Fred B. Samson

This issue of *The Wilson Bulletin* was published on 29 October 1981.

The Wilson Bulletin

Editor Jon C. Barlow

Department of Ornithology
Royal Ontario Museum
100 Queen's Park
Toronto, Ontario, Canada M5S 2C6

Assistant Editor Margaret L. May

Senior Editorial Assistants Gary Bortolotti
Nancy Flood

Editorial Assistants Keith L. Bildstein
C. Davison Ankney
Richard R. Snell
James D. Rising

Review Editor Robert Raikow
Department of Biological Sciences
University of Pittsburgh
Pittsburgh, PA 15260

Color Plate Editor William A. Lunk
865 North Wagner Road
Ann Arbor, MI 48103

Suggestions to Authors

See Wilson Bulletin, 91:366, 1979 for more detailed "Suggestions to Authors." Manuscripts intended for publication in *The Wilson Bulletin* should be submitted in triplicate, neatly typewritten, double-spaced, with at least 3 cm margins, and on one side only of good quality white paper. Do not submit xerographic copies that are made on slick, heavy paper. Tables should be typed on separate sheets, and should be narrow and deep rather than wide and shallow. Follow the AOU Check-list (Fifth Edition, 1957) and the 32nd Supplement (Auk, 90:411–419, 1973), insofar as scientific names of U.S. and Canadian birds are concerned. Summaries of major papers should be brief but quotable. Where fewer than 5 papers are cited, the citations may be included in the text. All citations in "General Notes" should be included in the text. Follow carefully the style used in this issue in listing the literature cited; otherwise, follow the "CBE Style Manual" (1972, AIBS). Photographs for illustrations should have good contrast and be on gloss paper. Submit prints unmounted and attach to each a brief but adequate legend. Do not write heavily on the backs of photographs. Diagrams and line drawings should be in black ink and their lettering large enough to permit reduction. Original figures or photographs submitted must be smaller than 22 × 28 cm. Alterations in copy after the type has been set must be charged to the author.

Notice of Change of Address

If your address changes, notify the Society immediately. Send your complete new address to Ornithological Societies of North America, % Sandra L. L. Gaunt, Box 21160, Columbus, Ohio 43221.

The permanent mailing address of the Wilson Ornithological Society is: c/o The Museum of Zoology, The University of Michigan, Ann Arbor, Michigan 48109. Persons having business with any of the officers may address them at their various addresses given on the back of the front cover, and all matters pertaining to the Bulletin should be sent directly to the Editor.

Membership Inquiries

Membership inquiries should be sent to Dr. Keith Bildstein, Department of Biology, Winthrop College, Rock Hill, South Carolina 29733.

CONTENTS

SUBSPECIES VS FORGOTTEN SPECIES: THE CASE OF GRAYSON'S ROBIN (*Turdus graysoni*)
Allan R. Phillips 301

HYPERPHAGIA AND SOCIAL BEHAVIOR OF CANADA GEESE PRIOR TO SPRING MIGRATION
M. Robert McLandress and Dennis G. Raveling 310

A MULTIPLE SENSOR SYSTEM FOR MONITORING AVIAN NESTING BEHAVIOR
James A. Cooper and Alan D. Afton 325

FORAGING SPEEDS OF WARBLERS IN LARGE POPULATIONS AND IN ISOLATION
Douglass H. Morse 334

DIFFERENTIAL PASSERINE DENSITY AND DIVERSITY BETWEEN NEWFOUNDLAND AND OFFSHORE GULL ISLAND ..... *Monique I. Vassallo and Jake C. Rice* 340

ENVIRONMENTAL INFLUENCE ON SOARING IN WINTERING RED-TAILED HAWKS
Charles R. Preston 350

BREEDING SUCCESS IN AN ISOLATED POPULATION OF ROCK DOVES
David E. Preble and Frank H. Heppner 357

RELATIVE ABUNDANCE OF GEORGIA CAPRIMULGIDS BASED ON CALL-COUNTS
Robert J. Cooper 363

NON-DRUMMING MALES IN A RUFFED GROUSE POPULATION ..... *Gordon W. Gullion* 372

GENERAL NOTES

BEHAVIORAL IMPLICATIONS OF ABERRANT SONG OF A RED-EYED VIREO
Jake C. Rice 383

COURTSHIP FEEDING AND COPULATION OF ROYAL TERNS ..... *Lawrence Kilham* 390

TWO CASES OF COMMENSAL FEEDING BETWEEN PASSERINES ..... *Mark B. Robbins* 391

FOOD FINDING IN BLACK-CAPPED CHICKADEES: ALTRUISTIC COMMUNICATION?
Millicent S. Ficken 393

THE SENTINEL CROW AS AN EXTENSION OF PARENTAL CARE
Gloria M. D'Agostino, Lorraine E. Giovinazzo and Stephen W. Eaton 394

BEHAVIOR OF A MALE LEAST BITTERN INCUBATING AFTER LOSS OF MATE
B. T. Aniśkowicz 395

NOTES ON BROWN PELICANS IN PUERTO RICO
Ralph W. Schreiber, David W. Belitsky and Bruce A. Sorrie 397

EGGS OF THE MARBLED MURRELET ..... *Lloyd F. Kiff* 400

FIRST DOCUMENTED CINNAMON TEAL NESTING IN NORTH DAKOTA PRODUCED HYBRIDS
John T. Lokemoen and David E. Sharp 403

FIRST RECORD OF THE BLACK-CHINNED HUMMINGBIRD IN ALBERTA
Philip H. R. Stepney and Peter C. Boxall 405

ORNITHOLOGICAL LITERATURE 407

REPORT OF THE CONSERVATION COMMITTEE—1980 438

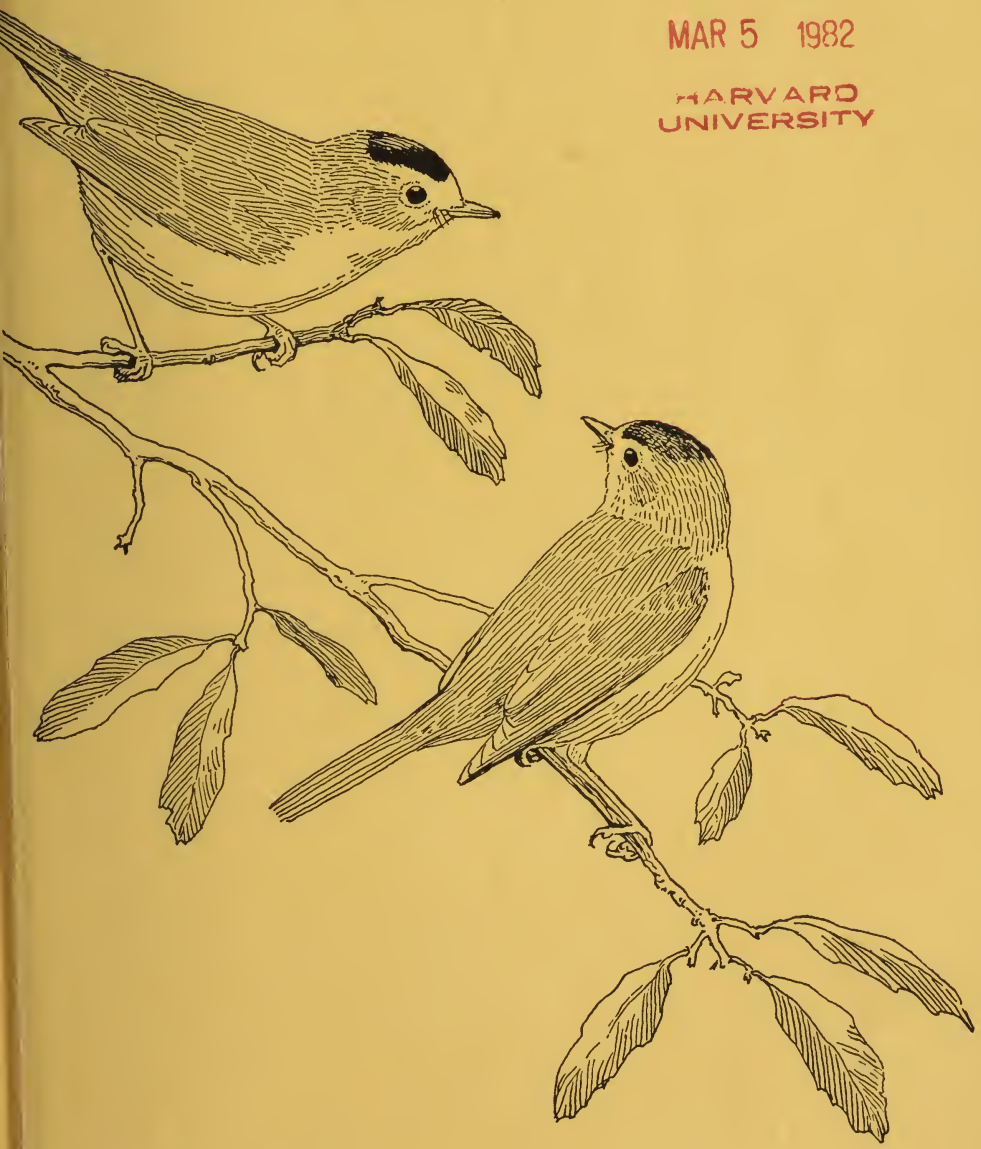
WIL
8424
.a

The Wilson Bulletin

PUBLISHED BY THE WILSON ORNITHOLOGICAL SOCIETY

VOL. 93, NO. 4 DECEMBER 1981 PAGES 457–609

MUS. COMP. ZOOL.
LIBRARY
MAR 5 1982
HARVARD
UNIVERSITY



THE WILSON ORNITHOLOGICAL SOCIETY

FOUNDED DECEMBER 3, 1888

Named after ALEXANDER WILSON, the first American Ornithologist.

President—Abbot S. Gaunt, Department of Zoology, Ohio State University, Columbus, Ohio 43210.

First Vice-President—Jerome A. Jackson, Department of Biological Sciences, P.O. Drawer Z, Mississippi State University, Mississippi State, Mississippi 39762.

Second Vice-President—Clait E. Braun, Wildlife Research Center, 317 West Prospect St., Fort Collins, Colorado 80526

Editor—Jon C. Barlow, Department of Ornithology, Royal Ontario Museum, 100 Queen's Park, Toronto, Ontario, Canada M5S 2C6.

Secretary—Curtis S. Adkisson, Department of Biology, Virginia Polytechnic Institute and State University, Blacksburg, Virginia 24061.

Treasurer—Robert D. Burns, Department of Biology, Kenyon College, Gambier, Ohio 43022.

Elected Council Members—Richard C. Banks (term expires 1982); Mary H. Clench (term expires 1983); Helen Lapham (term expires 1984).

Membership dues per calendar year are: Active, $16.00; Student, $14.00; Sustaining, $25.00; Life memberships $250 (payable in four installments).

THE WILSON BULLETIN is sent to all members not in arrears for dues.

THE JOSSELYN VAN TYNE MEMORIAL LIBRARY

The Josselyn Van Tyne Memorial Library of the Wilson Ornithological Society, housed in the University of Michigan Museum of Zoology, was established in concurrence with the University of Michigan in 1930. Until 1947 the Library was maintained entirely by gifts and bequests of books, reprints, and ornithological magazines from members and friends of the Society. Now two members have generously established a fund for the purchase of new books; members and friends are invited to maintain the fund by regular contribution, thus making available to all Society members the more important new books on ornithology and related subjects. The fund will be administered by the Library Committee, which will be happy to receive suggestions on the choice of new books to be added to the Library. William A. Lunk, University Museums, University of Michigan, is Chairman of the Committee. The Library currently receives 195 periodicals as gifts and in exchange for *The Wilson Bulletin.* With the usual exception of rare books, any item in the Library may be borrowed by members of the Society and will be sent prepaid (by the University of Michigan) to any address in the United States, its possessions, or Canada. Return postage is paid by the borrower. Inquiries and requests by borrowers, as well as gifts of books, pamphlets, reprints, and magazines, should be addressed to: The Josselyn Van Tyne Memorial Library, University of Michigan Museum of Zoology, Ann Arbor, Michigan 48109. Contributions to the New Book Fund should be sent to the Treasurer (small sums in stamps are acceptable). A complete index of the Library's holdings was printed in the September 1952 issue of *The Wilson Bulletin* and newly acquired books are listed periodically. A list of currently received periodicals was published in the December 1978 issue.

THE WILSON BULLETIN
(ISSN 0043-5643)

The official organ of the Wilson Ornithological Society, published quarterly, in March, June, September, and December. The subscription price, both in the United States and elsewhere, is $20.00 per year. Single copies, $4.00. Subscriptions, changes of address and claims for undelivered copies should be sent to the Treasurer. Most back issues of the *Bulletin* are available and may be ordered from the Treasurer. Special prices will be quoted for quantity orders.

All articles and communications for publications, books and publications for reviews should be addressed to the Editor. Exchanges should be addressed to The Joselyn Van Tyne Memorial Library, Museum of Zoology, Ann Arbor, Michigan 48109. Known office of publication: Department of Zoology, Ohio State University, 1827 Neil Avenue, Columbus, Ohio 43210.

Second class postage paid at Columbus, Ohio and at additional mailing office.

© Copyright 1982 by the Wilson Ornithological Society

Printed by Allen Press, Inc., Lawrence, Kansas 66044, U.S.A.

Capella gallinago, the Common Snipe, in spectacular ground display.
Photographed at a nest near Jackson, Michigan,
by Betty Darling Cottrille on 21 May 1967.

THE WILSON BULLETIN

A QUARTERLY MAGAZINE OF ORNITHOLOGY

Published by the Wilson Ornithological Society

VOL. 93, NO. 4 DECEMBER 1981 PAGES 457–609

Wilson Bull., 93(4), 1981, pp. 457–477

ON AERIAL AND GROUND DISPLAYS OF THE WORLD'S SNIPES

GEORGE MIKSCH SUTTON

While reading Leslie M. Tuck's monographic The Snipes: a study of the genus *Capella* some years ago, I found the chapter titled "Pair-formation and mating behaviour" especially interesting (Tuck 1972:167–179). Every word brought to mind the bewilderment I had felt while watching the courtship flights of Common Snipes (*Capella gallinago*). When, more recently, Betty Cottrille showed me her remarkable photograph of a Common Snipe displaying on the ground near its nest (see colorplate), my interest sharpened, for I had never witnessed any such performance myself. So explicit was the photograph that most of the tail's 16 feathers could easily be counted. The more I looked at that tail the more I wondered about the part it might take in aerial displays.

I first observed breeding Common Snipes in 1922. That spring, while studying the bird-life of Pymatuning Swamp, an extensive boggy woodland in northwestern (Crawford County) Pennsylvania (Sutton 1928), I was surprised to find snipes nesting in a cattail marsh near Hartstown, the village in which I was staying. The Common Snipe of North America was believed in those days to be of a different species from the Common Snipe of Eurasia and was widely known as Wilson's Snipe (A.O.U. 1931:110). On the very first evening of my sojourn (27 April), I heard many snipes "hooting." I had no idea that they were nesting in the area. I assumed that they were courting, that pairs were forming, that presently the whole noisy population would move on to breeding grounds in Canada. The hooting sounded like the rapid beating of wings. At times it was so sudden and loud that it was almost frightening. Since I had heard it many times before

entering the marsh, I knew that my being there had not started it, but when performing birds flew low over me, hooting loudly and shot off skyward at spectacular speed, I could not help feeling that I had been threatened with bodily attack.

Several days before finding a nest, I watched and listened eagerly, for though I had seen much of the Common Snipe before, its courtship behavior was new to me. On 3 May I observed a "new antic," a springing from the ground of a bird that "after a few energetic, direct wingbeats, put his wings high above his body, and describing a graceful arc, dropped toward the ground, his legs trailing, only to rise again to repeat the performance" (Sutton 1923). It did not occur to me that this was a "display." A bird collected just after performing the "new antic" proved to be a male. What I had witnessed has been called the "arched-wing display" of *C. gallinago* (Tuck 1972). According to this author, my description of it was the first to have been published.

Perusal of the literature convinces me that this "arched-wing display" has been witnessed many times in both North America and Eurasia, but it has been variously described and I may never have seen the whole of it. In Witherby et al. (1941), and also in Bannerman (1961), F. M. Ogilvie is credited with having seen a flying bird "sinking gently through air with raised wings and legs extended, as though about to alight, alternating with turning over first on one side then the other and ending with turning on back." Stubbs (1912) saw a performing bird in England "on some six different occasions twist completely over and proceed for some yards with outstretched wings belly uppermost." During my stay at Pymatuning Swamp in 1922 and in Iceland in 1958 (Sutton 1961) I never saw a Common Snipe turning "completely over" in this way.

What I did see, and in both places, was circling aerial display accompanied by fervent "hooting" or "bleating." In Pennsylvania all of the performing was done over cattail (*Typha*) marsh; in Iceland I observed it performed over flat, low-lying (but not marshy) meadow near Reykjavík (Sutton 1961). The display is an important part of courtship and pair formation and possibly of territory defense. "It occurs sporadically at any time of the year, but is most intense and continuous on the breeding grounds. It is mostly a male display, and males can be distinguished at this season by their frayed middle tail-feathers. The females bleat occasionally during early pair formation and usually after the laying of the first and second eggs" (Tuck 1972:167).

For years I have pondered this remarkable hooting or bleating, wondering whether it has ever been explained fully and correctly. Bahr (1907) wrote at length about it, naming several early writers who had expressed

their views about it, and paying special attention to a paper by Meves (1858) (translated from the Swedish by John Wolley) in which he discussed the "neighing sound which accompanies the single Snipe's . . . flight during pairing time . . . ." *C. gallinago* was sometimes called the Single Snipe in those days, presumably to distinguish it from the slightly larger Double Snipe (*C. media*), a species that breeds in Europe and western Asia.

What Meves (1858) had to say was thought provoking. According to him, opinions concerning the Single Snipe's "neighing" were varied: "Bechstein thought that it was produced by means of the beak; Naumann . . . that it originated in powerful strokes of the wings; but since Pralle in Hanover observed that the bird makes heard its well-known song or cry . . . at the same time with the neighing sound, it seemed to be settled that the latter is not produced through the throat. In the mean time, I have remarked with surprise, that the humming sound could never be observed whilst the bird was flying upwards, at which time the tail is closed; but only when it was casting itself downwards in a slanting direction, with the tail strongly spread out."

This paper's illustrations, pen-and-ink pictures that Wolley (1858) had "caused to be drawn" of what he called the "musical feathers of the tail" in six snipe species, are excellent. And entertaining indeed is Wolley's account of the way in which Meves, in "a little room in the middle of Stockholm," blew on these feathers and fixed them "on levers that he might wave them with greater force through the air," thus demonstrating how they produced the "deep bleat" of the male snipe and the "fainter bleat" of the female. As for the extra wide spreading of the outermost feather on each side of the tail, a spreading that has been illustrated by drawings from time to time (but never by photographs), neither Meves nor Wolley had anything to say. This outermost rectrix is slightly narrowed in most Common Snipes of North America and Eurasia, though not in all of them (see Tuck 1972:83, Fig. 24), and what has been written about aerial displays of snipes in general expresses almost universal belief that the narrowing of the one to several outer pairs of rectrices is responsible for the neighing.

Bahr's (1907) lengthy paper stated: (1) that in displaying Common Snipes observed by himself in England, the outermost rectrix on each side was spread so wide that it stood apart from the rest of the rectrices (1907:16, Fig. 3); (2) that the tail muscles of *C. gallinago* make possible this extra wide spreading of the outermost rectrix (1907:20, Fig. 20); and (3) that the two outermost rectrices, one on either side, though believed to be responsible for the neighing, are not by any means as conspicuously narrowed

(1907:18, 22; Figs. 4, 6) as they are in most other snipes, notably the Pintail or Asiatic Snipe (*C. stenura*), a species that breeds in eastern Siberia.

In my opinion, the importance of the narrowness of the outermost rectrix in *C. gallinago* has been overemphasized. In his scholarly paper on the aerodynamics of the Common Snipe's hooting, Carr-Lewty (1943) so stresses the strength, flexibility and narrowness of this outermost rectrix—in contrast to the wideness, weakness and inflexibility of the middle feathers—that I am puzzled by the photograph in Tuck (1972:83) of a 14-feathered tail in which the outermost rectrix on either side is almost, if not fully, as wide as the other 12. This tail is that of an "adult male" bird from Ireland. Might that particular bird have been incapable of hooting because its outermost rectrices were not narrowed? Not so, in my opinion. In my opinion, that bird hooted by fanning wide and depressing its whole tail, perhaps switching all 14 feathers from side-to-side as it went into a "power-dive." The tail of *C. gallinago* must indeed be equipped with powerful muscles, for in ground displays it is spread wide, lifted high and moved from side-to-side in a truly remarkable manner (see Williamson 1950 and colored frontispiece of this paper).

An important fact about the tails of the "true" snipes of the genus *Capella* may well be stated at this point: the number of rectrices in more than one species is remarkably inconstant. In the Forest, Marsh, or Swinhoe's Snipe (*C. megala*) of Asia the rectrices usually number 20, but "occasionally 18, 22, or even 26" (Tuck 1972:89). Of nine specimens examined for me by David M. Niles at the Delaware Museum of Natural History, four (2 males, 2 females) have 18 rectrices each, three (1 male, 2 females) 16 each, and only two (males) 20 each. In the Pintail Snipe the number is usually 26, "but individuals with 24 or even 28 have been recorded" (Tuck 1972:91). The two specimens at the Delaware Museum of Natural History represent the extremes: a male has 24 rectrices, a female, 28. In all "true" snipes, whatever the species, there is a tendency for the outer rectrices to be narrowed, but the tendency is less noticeable in the three geographical races long believed to constitute the species *C. gallinago* than it is in most other species. The breeding of these three races—*delicata* of North America, *faeroensis* of Iceland and the Faeroes, and nominate *gallinago* of continental Eurasia—is restricted to the northern part of the Northern Hemisphere.

Authors seem to agree that in *C. gallinago* vibration of the outer tail feathers—whether these are narrowed or not—is responsible for the hooting. Ludlow (Ludlow and Kinnear 1934), who observed courting Common Snipes in Chinese Turkestan, was so close to performing birds that he

"could see the vibration of the outer tail feathers." Yet Tuck's (1972:171) own words concerning the "somewhat frayed" condition of the "two central feathers" of the tail of a male that he netted in Newfoundland on 17 April 1960, finding that he had banded that very bird "three years previously at the same location," read as if he considered those two feathers themselves to some extent responsible for the bleating.

Be that as it may, there can be little doubt that the narrowed outer rectrices in most species of *Capella* play an important part in producing the sounds that accompany aerial displays. Morphologically, the most bizarre of the world's snipes assuredly is the Pintail Snipe, referred to above, in whose tail the 10 middle feathers are broad while the remaining eight pairs on each side become gradually narrower and stiffer, the outermost being mere spikes about 1 mm wide from base to tip.

The earliest account of this species' courtship may well be that of Popham (1898), who found the bird nesting along the Yenesei River in Siberia. Concerning the aerial part of its display he wrote: "I never heard the Pintailed Snipe utter any call when rising from its nest, but its 'drumming' sounds like bubbling water, while it is continued much longer and is far louder than the drumming of the Common Snipe. The bird works its way to a considerable height and then descends rapidly, 'drumming' as it goes; if close overhead the noise is terrific." Later, Popham (1901) summarized his observations thus: "The drumming of the Pintailed Snipe may best be described as resembling the sound made by unwinding the line from a salmon-reel with rapidly increasing speed."

More recently, Berman and Kuz'min (1965), as quoted by Tuck (1972:57), reported that male Pintail Snipes perform communally in toks, a tok being the aerial equivalent of a lek. Their words were: "Males in flocks of 10 to 15 birds flew impetuously. From time to time, the whole flock suddenly plunged sideways or each bird glided downwards. Maneuvering in a beautiful manner in the direction of the wind, turning from side to side, like large butterflies, the birds plunged more and more vertically, uttering short metallic calls, *tcheka-tcheka-tcheka*. As the speed of the birds increased the cries became increasingly more frequent, until they merged with the fizzing-and-whistling sounds which originated from the cutting of the air by the narrow tail-feathers. This sound became stronger, increasingly higher and longer, and each bird, descending almost to the ground, stopped dropping, soared upwards and caught up with the flock."

In their monumental Birds of the Soviet Union, Dement'ev, Gladkov and Spangenberg (1969) do not, surprisingly enough, have anything to say about the Pintail Snipe's communal displays. Basing their words on a

description by Dorogostaiskii, they state that the circling bird produces a sound like *chvin*, slowly repeated at first but gradually becoming "an uninterrupted trill of beautiful metallic sounds" and ending with a "sizzling" *chiz-zh*.

Most snipes currently placed in *Capella* have aerial displays, a notable exception being the Double or Great Snipe, a comparatively slow flying species whose courtship displays are largely, if not wholly, terrestrial and whose white tail corners are conspicuous as the male birds shuffle through the grass of the lek in the half-light (Blair, *in* Bannerman 1961). The species of *Capella* that do not have boldly white-cornered tails all take to the air when displaying. The aerial performances are accompanied by sounds, but how those who hear can be sure that certain sounds are vocal while others are not is beyond me. I am prepared to believe that some, perhaps all, of the windy, feathery, buzzing, fizzing, whistling, whirring, bleating, winnowing, neighing, or drumming sounds are produced by the whole tail or part of it, or perhaps by the wings and tail, although some of these sounds may be vocal to some extent.

Note that performing Solitary Snipes (*C. solitaria*) observed by Hume in India uttered a "loud, sharp, jerky call," then descended rapidly "with quivering wings and outspread tail, producing a harsh buzzing sound something like, but shriller and louder, than that produced by the Common Snipe" (Hume and Marshall 1881). Presumably that "loud, sharp, jerky call" was vocal, while the "harsh buzzing sound" was made by sudden fanning and depressing of the tail feathers. A much more recent observer, Baker (1929), also seemed to believe that *solitaria* made two different sorts of sound while performing. His words were: "In the breeding season they drum and bleat over their breeding-haunts like the Fantail [a common name, widely used in Asia, for the Common Snipe], being found at this season between 9,000 and 15,000 feet."

According to Dement'ev et al. (1969), who call *C. solitaria* the Hermit Snipe, performing males ascend, "flying smoothly like a bat and describing small circles; then, with wings half-folded and tail spread like a fan, the bird plummets downward. This is accompanied by sharp jarring sound, and as the drop is interrupted by several pauses, so too the sound is not continuous but intermittent. When still high above ground, the bird halts for an instant . . . and emits a loud cry, which may be taken for call of willow ptarmigan [*Lagopus lagopus*]. The sounds may be rendered as 'zhzhzh' . . . (brief pause) 'zhzhzh' . . . (brief pause) . . . 'zhzhzh' (longer pause) . . . 'chok . . . chok . . . chaaa,' the syllables 'chok . . . chok . . .' jerky, repeated in quick succession and 'chaaa' uttered after a brief pause, drawn out and nasal. After this the male again soars upward, again plummets downward, and so on, several times in succession. This mating

activity has much in common with that of Forest Snipe, but Hermit Snipe male [gives] louder calls and flies higher, not descending to treetops." The tail of *C. solitaria* usually has 20 rectrices (sometimes 22 or 24), the 3–6 outer pairs of which are narrowed.

Concerning the aerial displays of the Japanese, Latham's or Australian Snipe (*C. hardwickii*), a species with 18 tail feathers, the outermost three pairs of which are narrowed, Bahr (1907) quotes thus from the notes of a "Mr. Alan Owston, of Yokohama," who had sent him a skin of the species: "They breed on the grassy moorland at the foot of Mt. Fugiyama, at an elevation of 2000–3000 ft. above the sea . . . . When alarmed they fly . . . overhead, circling round generally against the sun, and every now and again they begin to cry 'chip, chip, chip, sheep, cheo, che-cheo,' and then rush downwards at the intruder, beating the air in the descent and making a terrific rushing noise." Owston also sent Baker this extract from T. W. Blakiston's "Birds observed on the southeast coast of Yezo [Hokkaido] in May," an article published in the Japanese journal *Chrysanthemum* for November 1882: "The Australian species act very like the Snipe of North America, by flying round pretty high and making sudden descents almost to the ground, which latter movement is accompanied by a whisping noise."

More recently, Fennell (1953) calls the courtship performance of *C. hardwickii* a "circular flight, some 25 to 30 feet above the ground, accompanied by a rather harsh *zrack*, *zrack*, *zrack* note uttered quite regularly and interrupted only by the rapid gă, gă, gă, gă, gă, gă, gă, gă, gă, gă, accompanying the frequent power dives. The latter call has a rather weird, feathery quality and increases in both tempo and volume as the bird nears the ground. A halting sort of choke interrupts the series of notes some three or four syllables before the end, adding to the feeling of rush and stumbling haste. None of the performers appeared actually to alight on the ground at the end of this dive but seemed to veer off and rise into the air to continue the circling flight." Here the author calls the *zrack* a "note" and the *gă* both a "call" and a "note," making us suspect that both sounds might be vocal. For me the word "feathery" describes a non-vocal hooting, drumming, or winnowing not unlike that of the Common Snipe, a sound produced by the spread tail. As for the *zrack*, I can only guess that it is wholly vocal. Since *C. hardwickii* winters widely in Australia (Peters 1934), it has from time to time been called the Australian Snipe.

The Forest or Swinhoe's Snipe, found by Gardner (1930) to be the "most abundant" of the snipes "from September to February" in paddy fields in the Philippines, was said by him to make a "whistling or, better, winnowing sound." As observed by Kozlova (1932) on its breeding grounds in northern Mongolia, the species "soars up into the air to an immense

height, uttering sounds something like 'tchiki-tchiki-tchiki'; then it descends again with great rapidity, producing a clear whistling or howling noise. At about 7 A.M. it seems to become tired of its play, and, sitting on some dry trunk of a tree, continues only its 'tchiki-tchiki,' without soaring up into the air." The 'tchiki-tchiki' obviously is vocal and I strongly suspect that the "whistling or howling noise" is non-vocal. A translation in Tuck (1972:55) from Koslov's "Fauna of the USSR" elaborates a bit, explaining that the performing bird "ascends in spirals, closes its wings, spreads its tail and plunges downward, making first a low, then a constantly louder noise as from a rapidly twirling metallic object."

Dement'ev et al. (1969) state that the courting Forest Snipe produces a sound like *chvi* or *chchvi* as it describes "part of a circle" then "half folds its wings behind back and, with a slight loss of height and speed beats its wings and begins flying horizontally. It then begins a sudden drop accompanied by a sharp sound resembling rustling of paper kite." In the Forest Snipe's tail the outermost four or five pairs of rectrices are narrowed (see figure in Tuck 1972:59).

The Wood or Himalayan Snipe (*C. nemoricola*), a somewhat chunky, slow flying species that breeds "in the Himalayas, between 2,000 and 12,000 feet, from northeastern Punjab to the southern Shan States" (Peters 1934); that has been recorded in winter southward to "southern India, southern Assam and Burma" (Peters 1934); that Adams (1858), who called it the Solitary Snipe, considered a bird of "lonely glens . . . where the pine grows tall and dense, and the sun's rays seldom penetrate"; and that Irby (1861) found "in little rushy patches of bog on the sides of the hills, never on streams" in May 1859 at 6000 to 7000 feet in the Province of Kumaon [in the State of Uttar Pradesh in northern India, just west of northern Nepal] is surely among the least migratory of the Northern Hemisphere's snipes. It is "probably a resident bird throughout the lower Himalayas . . . between 6,000 and 2,000 feet" (Baker 1929). According to Ludlow and Kinnear (1937), the many Himalayan Snipes observed "in the hills west of Mago [on accompanying map shown as a district, not a town, in eastern Tibet] in early August" were "flighting like Woodcock of an evening, uttering a croaking 'chur, chur' call." I hazard the guess that this 'chur, chur' was a non-vocal sound produced by spreading and depressing the tail. The species has 18 rectrices, the outermost three or more pairs of which are narrowed.

Of the seven species of *Capella* thus far discussed, only *C. gallinago* breeds in both the Old and the New World. The three above-mentioned races of *C. gallinago* are all strongly migratory, moving southward in winter to areas largely south of the breeding grounds (see map *in* Tuck 1972:107). The species' spread across two large continents throughout an

area cold enough in winter to require extensive migration bespeaks hardihood, aggressiveness and reproductive potential unique within the genus. Tuck (1972:9–10 et seq.) obviously believes that these attributes have led the species to establish breeding populations also in southern parts of the world, a concept that I find acceptable not only because the southern forms are much like the three northern ones morphologically—though in all of them, without exception, the outermost rectrices are more conspicuously narrowed than they are in *delicata*, *faeroensis* and nominate *gallinago*—but also because the aerial part of their courtship behavior is much the same.

Tuck was not, of course, the first ornithologist to believe that some of these southern snipes might be subspecies of *gallinago*. Seebohm (1886), whose paper on "the species of the genus *Scolopax*" dealt chiefly with morphology rather than behavior, long ago had this to say: "The last half-dozen [southern] species or subspecies . . . can scarcely be regarded as more than tropical forms of the Common Snipe. They vary very slightly in colour or pattern of colour, the variations between the species being scarcely greater than those within each species."

The five southern snipes that are, in my opinion, races of *C. gallinago* are *paraguaiae*, *magellanica* and *andina* of South America and *nigripennis* and *angolensis* of Africa. Whether all five of these are worthy of recognition is beyond the scope of this paper, for I have made no attempt to borrow series of specimens for comparison, measurement, etc. The five southern races resemble the three northern ones closely in proportions, color and size. Considered together, they and the three northern races form a composite aggregate quite different from any of the six other northern species discussed above, and they are sufficiently different from the Madagascar Snipe (*C. macrodactyla*) of Madagascar and Mauritius, and the Páramo Snipe (*C. nobilis*) of the northern Andes to form a discrete conspecies. I confess to being puzzled because breeding of the five southern races is not restricted to high southern latitudes as that of the three northern races is to high northern latitudes. Not one of the southern races is, so far as known, strongly migratory.

Let us see what observers have reported about these southern races of *C. gallinago*. The earliest comment on the courtship of *C. g. paraguaiae* may well be that of Durnford (1877), who, having watched the snipes in northern Argentina, had this to say: "During the spring they go through the same aerial movements as the Common Snipe at home, rising to a great height by a circling motion, and 'drumming' whilst descending in a diagonal line." Following this statement, Durnford asks a pertinent and thought-provoking question: "How is this curious habit to be accounted for in the South American and European forms except by the theory of

inheritance from a common progenitor?" Another early report on *paraguaiae* is that of Aplin (1894), who became acquainted with the bird in Uruguay. According to him, the form's drumming differed from that "produced by the English Snipe." He called the sound "a long shaking *kurrrrrr* (the sound can be produced to some extent in the back of the human throat); sometimes it varies to a deep low throated *gurrr* . . . ." Hudson, in his "Birds of La Plata" (1921), tells us that performing birds "produced singular grinding and scythe-whetting sounds . . . in their violent descent from a great height." In my opinion, the words "grinding" and "scythe-whetting" both aim at describing non-vocal sounds.

Wetmore (1926), discussing a "mating display" observed by him in Entre Rios, northern Argentina on 9 October 1920, wrote that the birds "flew swiftly 12 or 15 meters above the ground and suddenly extended the wings stiffly in a V-shaped angle above the back and fell laterally through the air for a considerable distance." How this graphic description of the "arched-wing display" takes me back to the hours I had with the snipes in northwestern Pennsylvania in the spring of 1922!

Pinto (1935), describing the behavior of *paraguaiae* observed by him in Bahia, eastern Brazil, says: "On moonlit nights it is wont to entertain itself making swift parabolas in space, when one hears a characteristic guttural noise that is responsible for the dismal name *Rasga-mortalha* [Death-rattle] by which it is known in some areas." A much more recent observer, Barlow (1967), who witnessed the "typical aerial courtship flights . . . each night and on overcast days" between 29 April and 13 May [1963] in Uruguay, called the sound that accompanied flights "winnowing."

Helmut Sick (in litt.), writing of *paraguaiae* observed on the snipe's breeding ground in Brazil, says that the displaying bird "makes a strong noise that reminds one of the bleating of a she-goat." The performance consists of phrases that ascend in pitch, each lasting 1 or 2 sec. The sound is produced by a "channeled current of air . . . conducted by the wings to the tail, which functions as a 'musical instrument'" (see Welty 1975:211). At the height of the breeding season, Sick tells us, male birds call *ke-ke-ke* or *pi-kjér*, *pi-kjér*, not from the air but from the ground.

On the courtship of *C. g. magellanica*, a subspecies that is "partially resident" in continental South America "from Chile . . . and Argentina . . . south to Tierra del Fuego" (Peters 1934); that Reynolds (1935) found "common enough" on Guffen, an islet just north of False Cape Horn; and that Woods (1975) found "fairly common" on the Falkland Islands, little has been published. Cawkell and Hamilton (1961), writing of birds heard on the Falklands, report: "The drumming note, made in flight, is decidedly musical and is produced only at dusk or in the night." According to Tuck (1972:53), a Reynolds manuscript comments "that sportsmen who are familiar with both *gallinago* of England and *magellanica* cannot differen-

tiate between the bleating of the two." Woods (1975) states that Falkland Islands birds in "nocturnal display-flight" circle high in the air "producing a musical bleating sound with the spread rigid outer tail feathers."

The small subspecies *C. g. andina*, which presumably is largely resident in bogs of the high Andes of southern Peru, western Bolivia, northern Chile and northwestern Argentina (Meyer de Schauensee 1970), is considered a full species by some taxonomists. Nothing seems to have been published about its courtship behavior. Judging from what has appeared in print about its ecology and distribution, I suspect that it is locally sympatric with the Páramo Snipe along the southernmost edge of the range of that much larger and perhaps more slender species. About the Páramo Snipe itself, more later.

Concerning the subspecies *C. g. nigripennis*, a bird long known as the African or Ethiopian Snipe, whose "drumming or bleating noise" is "much the same" as that of the Common Snipe in Europe (Mackworth-Praed and Grant 1952), and whose Mallophaga are "identical" with those of the European form (Meinertzhagen 1952), Thomas Ayers (*in* Gurney 1868) had this to say of courting birds observed in Natal, South Africa: "At this season the cock birds are a great deal on the wing—evidently wooing. They fly about like so many Swallows—rising in the air, and descending with a rapid sweep and beat of the wings to within a few feet of the ground, then rising again and repeating the movement, at the same time making a curious, loud, vibratory, rushing noise, which I once heard as late as midnight on a still moonlight night. The cock birds on the ground almost incessantly utter a loud 'chuck, chuck.' " Gurney (1864) himself said that the flight of *nigripennis* was "precisely like that of the common English Snipe."

Cheesman and Sclater (1935), having observed the courtship of *nigripennis* in northwestern Ethiopia, report: "The drumming cruise takes place not more than 30 feet in the air in circles of 300 yards in diameter. As they fly they fall and make a whirring noise, repeated six times. The fall takes them almost to the ground; then they rise again and repeat the performance. The note produced does not seem as high pitched as that of the English Snipe, and does not resemble a bleating goat, but rather the wing-beat of a swan flying in the distance, but more rapid." According to Breslford (1947), who found the snipes on "sand-bank" islands in Lake Bangweulu in northern Rhodesia, their "drumming" was heard . . . in July.

I suspect that the "chuck, chuck" reported by Ayers (*in* Gurney 1868) was vocal and that the "curious, loud, vibratory noise" was that of the flying bird's tail spread to its fullest and pushed downward. In view of what has been reported about the Double Snipe's use of its white tail-corners in terrestrial display (Bannerman 1961), I was prepared to find

that *nigripennis*, with its largely white outermost rectrices, would also be content with displaying on the ground—not so, apparently.

Concerning the race *C. g. angolensis*, a very long-billed form said to breed from "Angola to Ngamiland and Northern Rhodesia, east to Ndola" (White 1945), I have no comment, since I do not know what its range is now known to be. Some of what is quoted above may have to do with *angolensis* rather than *nigripennis*.

So much, then, for the species *C. gallinago*, the one snipe of the world that breeds in both the Northern and Southern hemispheres, and for six of its congeners that breed only in the Northern Hemisphere. The congeners that breed wholly or largely in the Southern Hemisphere include the Madagascar Snipe, already mentioned, a large, slow-flying form endemic to Madagascar and Mauritius, and a remarkable congeries of South American forms ranging in size from that of the fairly large Páramo Snipe, above mentioned, through that of the slightly larger Imperial, Banded, or Bogotá Snipe (*C. imperialis*), which is known from only two or three localities in the mountains of Colombia and Peru, and through that of the still larger Andean Snipe (*C. jamesoni*) and Cordilleran Snipe (*C. stricklandii*), respectively of the northern and southern Andes, to that of the strikingly big Giant Snipe (*C. undulata*) of the northern part of the continent. *C. jamesoni* and *C. stricklandii* may be conspecific: they resemble each other in many ways and are nowhere sympatric (see Meyer de Schauensee 1970). My calling *C. nobilis* the Páramo Snipe, rather than the Noble Snipe, follows Phelps and Phelps (1958), who gave it the Spanish common name Becasina Paramera. Páramo Snipe is a meaningful name, whereas Noble Snipe is not.

To be noted is the fact that while the above-named Southern Hemisphere forms vary greatly in size, no species in that part of the world has rectrices by any means as highly specialized as those of the Pintail Snipe. Taxonomically, the most puzzling of the Southern Hemisphere forms are *C. macrodactyla* and *C. nobilis*, species which are so much alike that one early systematist considered them conspecific despite their being a continent removed from each other (Seebohm 1886). Admittedly it is difficult to see why, if the process of evolution eventuates in two races of *C. gallinago* in continental Africa, it should not also eventuate in a third one in Madagascar; but *macrodactyla* is not only proportionately longer-billed and longer-legged than *gallinago*, it is different in behavior. From November 1942–April 1944, van Someren (1947) saw much of *macrodactyla* in the mountains near Fianarantsoa, Madagascar. He considered its flight "quite unlike the sharp zigzagging of the European Snipe." On 23 November he flushed a parent bird from a small chick whose "clambering and

running through the long grass" was "unlike the cryptic behaviour of the chicks of the Common Snipe."

I find no comparable statements about the behavior of the Páramo Snipe, a bird that may, for all that is now known, be sympatric with *C. g. andina* in the northwesternmost part of that bird's range. Assuredly no specimens indicating even the slightest intergradation between the two forms have been reported.

Certain basic attributes common to the habitats of *macrodactyla* and *nobilis*—chilly nights at the high bogs, food hard to reach in the deep mud—evidently have continued for so long to favor the survival of heavier, longer-billed, longer-legged individuals that both forms have come to be much tougher than Common Snipes, this despite obvious similarities in colors and patterns of plumage. The fact that the two resemble each other superficially suggests that evolutionary forces have operated in much the same way in two far-apart yet ecologically congruous areas. One can but wonder what the precise habitat-differences may be between *C. nobilis* and *C. g. andina* in the montane area throughout which their ranges abut or overlap; the latter is such a little bird in comparison!

The "nuptial flight song" of the Madagascar Snipe, as heard on 9 September 1930, at Doany, Madagascar, by Rand (1934), was "similar to that of *Capella delicata* [*Capella gallinago delicata* of this paper]"—a comment that seems to argue for calling *macrodactyla* a race of *gallinago*. But if, as Rand states, the native names of the bird, Hárakáraka and Ráva rára, are indeed "imitations of the flight song," I cannot help feeling that the sounds most often accompanying aerial courtship must differ radically from the Common Snipe's *hu-hu-hu-hu-hu* that I have heard so many times. Rand (1934) may have erred in supposing that the native names imitated the flight song. According to Harting (1882), the name used by natives at Fianarantsoa was *kekekeka* (presumably in imitation of a call given from the ground), the name *rava-rava* being used not for any "true" snipe, but for the Painted Snipe (*Rostratula benghalensis*). As for the spelling *rava-rava*, rather than *ráva rára*, see Newton (1865).

Almost nothing has been published on the behavior of the Páramo Snipe, a species found by Moore (1934) to be "the most conspicuous bird" in a valley at 11,000 feet in the vicinity of Mt. Sangay in the Ecuadorean Andes. Moore's statement that "at sundown" the snipes' "ecstatic forms whirled overhead to the accompaniment of strange sounds that reminded one of a deep-pitched policeman's rattle" may not pertain at all to the Páramo Snipe, for an elderly Indian of Moore's party insisted that the sound was made by a much larger bird, the sympatric Andean Snipe. Whether what Moore heard was Páramo Snipes or Andean Snipes (or both!), the sound

could not have been much like that of courting *C. gallinago*. According to Harry Lumsden, who heard the Páramo Snipe's "bleating" in Colombia, the sound was "very low and deep in tone" (Tuck 1972:57).

The Strickland's or Cordilleran Snipe (*C. stricklandii*), as observed by Reynolds (1935) on six of the Wallaston Islands at South America's southernmost tip between 11 and 22 December 1922, was "heard continuously throughout the night . . . when the wind was not roaring." On Herschel Island, while one bird was "drumming" overhead, another bird, thought to be the female, "kept up a continuous 'chip-chip-chip' etc. from the ground." This same "chip-chip-chip" was "uttered frequently in flight," followed by drumming of such exceedingly low pitch as almost to reach "the lowest limit of human audibility." A loud *cha-wheu* or *cha-whoo, cha-whoo, cha-whoo* repeated a number of times was distinctly audible when the drumming could "no longer be picked up." How Reynolds (1935) knew that the drumming was continuing when he could no longer hear it is not clear to me. In my opinion, the *cha-whoo* was produced by the outspread tail, which has 14 feathers, none of them noticeably narrowed or stiffened (see figure *in* Tuck 1972:71).

The Andean or Jameson's Snipe (*C. jamesoni*) of the northern Andes, as observed by Vuilleumier (1969) in "wooded thickets and grassy openings at altitudes from 3,300 to 3,400 m." in the Bolivian Andes, gave a double note, a *whee-tschwu*, "repeated at a frequency of about two per second, while the calling bird flies in wide circles on a level course." After calling constantly for 30 sec to a full minute, the circling bird began to descend, slowly at first, but gaining speed. As it neared the ground a "muffled, low-pitched sound which vaguely reminds one of a cow's bellow" became audible. Vuilleumier (1969) presumed that this low-pitched sound was "produced by the vibration of feathers, and not vocally, although neither tail nor wing feathers show obvious modifications." To be noted is the significant fact that the second syllable of this *whee-tschu* of *jamesoni* rhymes with the *cha-whoo* of *stricklandii* (see paragraph above). The tail of *jamesoni* also has 14 feathers, the outermost three pairs of which are somewhat narrowed in a specimen from Colombia (USNM 386788) at hand. If the outermost rectrices are narrowed in most *jamesoni* but not in most *stricklandii* the difference would, in my opinion, argue for calling the two forms separate species.

The aerial displays of the little known Imperial Snipe (*C. imperialis*), as witnessed in July 1968 "just below the timberline at 3,300 m (10,000 feet)" in the "vast and largely unexplored northern massif of the Cordillera Vilcabamba" of central Peru, were "of equal intensity at dawn and dusk," reaching "peak intensity" in clear weather, "heavy cover almost entirely squelching the usual performance." The display flight was accompanied

by a "song" that began "with a series of rough staccato notes that rapidly increase in volume. A climactic middle section is marked by a complex rhythmic pattern of double and triple notes. After a final triple burst, the song enters a terminal phase in which the sound intensity diminishes in a sequence of evenly spaced notes" (Terborgh and Weske 1972). These authors obviously believed this "song" to be wholly vocal. According to them, the "first two-thirds" of it, "comprising the crescendo and climactic phases, are given in level flight powered by rapid shallow beats of the stiffly held wings. A gently sloping dive commences with the terminal sequence of single notes. An instant after the last note of the vocalization the bird pulls sharply out of the dive, producing a rush of air through the remiges (?) that is clearly audible at close range."

The "rush of air" might, in my opinion, have been through the widespread and depressed tail feathers, an opinion based on my belief that in most species of *Capella* the rectrices are used in this way. Terborgh and Weske (1972) consider the aerial display of *imperialis* similar "in several respects" to that of *jamesoni* (see quoted material above); they say nothing about the courtship of the big snipe of the southern Andes as such, for they consider *jamesoni* a geographical race of *stricklandii*. Concerning *imperialis* and "*C. stricklandii jamesoni*" they have this to say: "Both species display after sundown well into darkness and call repeatedly while flying in wide nearly level circles"; vocalizations of *jamesoni* "are apparently given continuously for several circuits," while those of *imperialis* "are more complex and divided into discrete episodes. Both species produce a low whirring sound while descending, presumably by allowing air to pass through the remiges in a certain way"—*imperialis* "at the end of each song bout," *jamesoni* "at the termination of a 30- to 60-second display period as it spirals back to earth."

I cannot dismiss from discussion these three large, somewhat stocky South American snipes—*imperialis*, *jamesoni*, and *stricklandii*—without mentioning the fact that Peters (1934) placed them in the genus *Chubbia*, a taxon erected by Mathews (1913). Insofar as their courtship behavior is concerned, there seems to be some justification for considering *Chubbia* a valid genus. The three species resemble woodcocks of the genera *Scolopax* and *Philohela* in being proportionately shorter-tailed and shorter-winged than the several other snipes discussed in this paper.

Now for the dramatically big Giant Snipe (*C. undulata*), a bird whose habits have been virtually unreported. The species' disproportionately short tail has 14 feathers, the outermost two or three pairs of which are somewhat, though not noticeably, narrowed (see figure *in* Tuck 1972). Helmut Sick (in litt.), writing of the bird's behavior as observed by him in Brazil, tells us that it is "by nature lazy"; that, rather than flushing, it

"squats or escapes by walking slowly, taking long steps"; that it is "even more nocturnal" than its sympatric congener, *C. g. paraguaiae*; and that it does most of its performing on "hot rainy nights." In courtship displays "high above its territory" it produces a sound that resembles the phrase hó-go, go or gá-ga, ga, loud at the beginning, but trailing off at the end, and with a timbre so much like that of the human voice that one cannot help feeling that it is vocal. The sound, whether vocal or not, is responsible for the vernacular names Água-só, O-rapaz and Rola-pau. In addition to this trisyllabic phrase, the bird produces a "strong droning *sch* that lasts four seconds, a sound that might be compared to . . . the buzzing of a large swarm of bees." The general appearance of this very large snipe certainly calls woodcocks to mind. In the one specimen of the species at hand, the rectrices are hard to count for they are hidden by the long and abundant coverts.

The little Jack Snipe (*Lymnocryptes minimus*) of Eurasia is sometimes placed in *Capella* (Edwards 1974), but it is so unlike the several other snipes already discussed that it may well belong in a genus by itself. It is famous for the "cantering" sounds that it makes while courting. It has only 12 tail feathers, all soft and somewhat pointed, none noticeably narrowed. The "cantering," which has been transliterated as "lock-toggi, lock-toggi" and "clockety-clockey, clockety-clock" by Blair (*in* Bannerman 1961), and which must be vocal since it is given from the ground as well as from the air, is not, apparently, analogous to the bleating, hooting, or drumming of *C. gallinago* and most of that bird's congeners.

According to Blair (*in* Bannerman 1961), the Jack Snipe was once known in parts of its extensive range as the Silent Snipe, for it was believed to be voiceless during fall and winter, but "in the breeding season, though difficult as ever to flush," it made its presence known "by what must rank as one of the most peculiar notes uttered by a bird"—notes that take on "a liquid quality, bearing some resemblance to the bubbling of a spring, or even to the boiling of a kettle." Such Jack Snipe courtship noises as are comparable to the bleating of the Common Snipe, are, according to Blair, made as the flying bird "glides down on outstretched wings, its quills meanwhile producing a whirring sound reminiscent of the drumming of its ally." I feel sure that the word "quills," as used here, refers to wing quills, not tail quills. Unlike most of the snipes discussed in this paper, the Jack Snipe does not use its tail at all in producing a sound while in courtship display.

Finally, a word about the Common Snipe picture that set me to writing this paper (see colorplate). The photograph was taken on 21 May 1967, near Jackson, Jackson Co., southern Michigan, by Betty Darling Cottrille. It shows a bird with lifted, widespread tail displaying at the nest. The

fluffy coverts look like under tail coverts, but they are upper coverts. After holding the tail in this position for a second or so, the snipe turned it so that the under side, with the coverts, faced the camera.

Betty Cottrille and her husband, Dr. W. Powell Cottrille, have been enthusiastic observers of birds for a long time. The Common Snipe has nested regularly in a marshy area not far from their home in Jackson. For 14 successive seasons, beginning in 1952, the Cottrilles paid special attention to that species. Nest after nest that they found held a full clutch of four eggs. What they wanted was a nest ready for eggs or with an incomplete clutch so that they could observe the birds' behavior during the incubation period. By 1967 their search had become almost an obsession.

Let me now quote from Betty Cottrille (in litt.) herself: "That year [1967] a pair with early nest weathered the vicissitudes of cold, rain, and finally, on 23 April, a three-inch snowfall. Hatching began late in the day on 13 May. Next morning, which was overcast and chilly, we found one egg in the nest and three chicks dispersed in the grass with their parents. Meanwhile, we had discovered another nest, this with one egg on 4 May and four eggs on 7 May. Having learned from Bent's [1942: 86] classic work that incubation would last 18–20 days, we made plans."

"On 21 May, the 15th day of incubation, the weather was perfect for photography. My husband and I, he with a movie camera, I with a 'still,' spent 1 ¾ hours in the blind that morning, hoping that the bird on the nest would exhibit some variation in behavior now that the end of the incubation period was at hand. The blind was about ten feet from the nest. Our cameras were poised. The incubating bird, obviously at ease while we waited, took several short naps, with bill-tip resting on the ground."

"What a surprise was in store for us! When the bird decided to leave the nest it stood up, took a few steps away from the eggs, leaned forward, and displayed. The display involved, first, spreading and lifting the tail until it stood straight up, then slowly, not jerkily, turning the perfect fan until, with upper side and coverts facing the camera, its plane paralleled that of the body's main longitudinal axis. Nor was this all. Having held the bizarre position for a second or two, the tail swung back to 'normal,' then turned once more—through an arc of 90 degrees—this time presenting its under side and coverts to the cameras. We were indeed fortunate: my husband's movies, as well as my stills, recorded what we had witnessed."

"On the 19th day of incubation (25 May) luck was with us again, but of a different sort. The weather was just right. When we visited the nest early that morning it contained four chicks, two of them dry, the other two still wet, with their shells nearby. The parents were beside themselves

with excitement. Within minutes we had set up the blind and focussed cameras, anticipating a repeat of that spectacular display. No such luck this time, for the emphasis had shifted to caring for the chicks. One parent darted in and out of the grass, which was now tall, clucking and dropping its wings, occasionally running to the brood and covering them hurriedly. As the two youngest dried and fluffed out, the chicks became more active. Now the parents, hidden in the grass, seemed to increase their coaxing. One by one the chicks tottered and stumbled to them. Out of sight—the excitement over! Nothing remained, except the flattened grass where the blind had been, to bear witness to that unforgettable drama. How the pictures would remind us of the wonderful antics we had witnessed so many times spring after spring!"

SUMMARY

All but one of the 13 currently recognized species of the scolopacid genus *Capella* display in the air during courtship, though aerial display is not restricted to the breeding season. Display flights are accompanied by hooting, bleating, neighing, or whinnying sounds that are widely believed to be nonvocal and that almost certainly are produced by vibration of some or all of the tail feathers. Drawings showing extra-wide spreading of the narrowed outermost feather on each side of the tail in *C. gallinago gallinago* have led to the belief that that feather is responsible for the sound; but investigation reveals the fact that this feather is not by any means always much narrowed in the Northern Hemisphere's three races of *C. gallinago*; that in the several Southern Hemisphere races of *C. gallinago* 2 or 3 pairs of outer rectrices are narrowed; that in several other species of *Capella*, notably *C. stenura*, one to several outermost pairs of rectrices are narrowed; and that in ground displays of *C. gallinago* in various parts of that species' very wide range the movements of the tail reveal such great maneuverability as to suggest that the hooting or neighing is produced by the pressing downward or from side to side of the whole tail. Courtship flights of the Giant Snipe (*C. undulata*), hitherto unreported, are like those of smaller snipes in some ways but are accompanied by trisyllabic sounds that are probably vocal. The courtship of *C. gallinago andina*, a form that inhabits the Andes, apparently has not been described. The Double Snipe (*C. media*), whose outer rectrices are largely white, displays on the ground rather than in the air. The Jack Snipe (*Lymnocryptes minimus*), a small species placed by some taxonomists in *Capella*, makes strange "cantering" sounds during courtship, but since these are given from the ground as well as from the air they are presumably vocal.

ACKNOWLEDGMENTS

The following are to be thanked for their assistance in preparing this paper: Betty Darling Cottrille, for her fine photograph of the displaying snipe and for her account of taking the picture; personnel of the U.S. National Museum and the Carnegie Museum of Natural History for lending specimens; David M. Niles, for counting the rectrices of snipe specimens at the Delaware Museum of Natural History; Helmut Sick, for material on *Capella undulata* that will appear in his forthcoming book on the birds of Brazil; Norman Boke and Loretta Nickel for translating textual material from the Portuguese; Robert M. Mengel for looking up certain references; John Farrand and John S. Weske for checking all of my statements about *Capella imperialis*; Olin Sewall Pettingill, Jr., and David F. Parmelee, for information of *Capella*

gallinago magellanica; and D. Scott Wood for borrowing needed specimens and for counting the rectrices of some of these.

LITERATURE CITED

Adams, A. L. 1858. Notes on the habits, etc. of some of the birds of India. Proc. Zool. Soc. London 466–512.

Aplin, O. V. 1894. On the birds of Uruguay. Ibis 6:149–215.

American Ornithologists' Union. 1931. Check-list of North American birds, 4th ed. Lord Baltimore Press, Baltimore, Maryland.

Bahr, P. H. 1907. On the "bleating" or "drumming" of the Snipe (*Gallinago coelestis*). Proc. Zool. Soc. London 12–35.

Baker, E. C. S. 1929. The fauna of British India, including Ceylon and Burma. Birds, Vol. 6. London, England.

Bannerman, D. A. 1961. The birds of the British Isles. Vol. 9. Oliver and Boyd, London, England.

Barlow, J. C. 1967. Autumnal breeding of the Paraguay Snipe in Uruguay. Auk 84:421–422.

Bent, A. C. 1942. Life histories of North American shore birds. U.S. Natl. Mus. Bull. 142.

Berman, D. I. and I. F. Kuz'min. 1965. Pintailed Snipe in Tuva. Ornithologica 7:209–216. Transl. from Russian by Canadian Wildlife Service.

Breslford, V. 1947. Notes on the birds of the Lake Bangweulu area in northern Rhodesia. Ibis 89:57–77.

Carr-Lewty, R. A. 1943. The aerodynamics of the drumming of the Common Snipe. Br. Birds 36:230–234.

Cawkell, R. A. and J. E. Hamilton. 1961. The birds of the Falkland Islands. Ibis 103: 1–27.

Cheesman, R. E. and W. L. Sclater. 1935. On a collection of birds from north-western Abyssinia, Pt. 2. Ibis 77:297–329.

Dement'ev, G. P., N. A. Gladkov and E. P. Spangenberg (eds.). 1969. Birds of the Soviet Union. Vol. 3. Publ. for Smithsonian Inst. and N.S.F., Washington, D.C. by Israel Prog. for Sci. Transl. (Jerusalem).

Durnford, H. 1877. Notes on the birds of the Province of Buenos Ayres. Ibis 19:166–203.

Edwards, E. P. 1974. A coded list of birds of the world. Private publ., Sweet Briar, Virginia.

Fennell, C. M. 1953. Notes on the birds of Daikokujima, Hokkaido, Japan. Condor 55: 38–52.

Gardner, L. L. 1930. The whistling of snipe. Condor 32:164–165.

Gurney, J. H. 1864. A sixth additional list of birds from Nepal. Ibis 6:346–361.

———. 1868. An eighth additional list of birds from Nepal. Ibis 10:40–52.

Harting, J. E. 1882. On the eggs of some rare wading birds from Madagascar. Proc. Zool. Soc. London 353–357.

Hudson, W. H. 1921. Birds of La Plata, Vol. 2. J. M. Dent & Sons, Ltd., London, England.

Hume, A. O. and C. H. T. Marshall. 1881. The game birds of India, Burmah, and Ceylon, Vol. 3. A. O. Hume and C. H. T. Marshall, Calcutta, India.

Irby, L. H. 1861. Notes on birds observed in Oudh and Kumaon. Ibis 3:217–251.

Kozlova, E. V. 1932. The birds of south-west Transbaikalia, northern Mongolia, and central Gobi, Pt. 3. Ibis 74:567–596.

Ludlow, F. and N. B. Kinnear. 1934. A contribution to the ornithology of Chinese Turkestan, Pt. 4. Ibis 76:95–125.

——— AND ———. 1937. The birds of Bhutan and adjacent territories of Sikkim and Tibet, Pt. 3. Ibis 79:467–504.

MACKWORTH-PRAED, C. W. AND C. H. B. GRANT. 1952. The birds of eastern and north-eastern Africa, 1st ed., Vol. 1. Longmans, London, England.

MATHEWS, G. M. 1913. The birds of Australia, Vol. 3. H. F. and G. Witherby Ltd., London, England.

MEINERTZHAGEN, R. 1952. Systematic relationships between Old-world birds. Ibis 94:545–546.

MEVES, W. 1858. On the Snipe's "neighing" or humming noise, and on its tail-feathers' systematic value. (Transl. from Swedish by J. Wolley.) Proc. Zool. Soc. London 199–203.

MEYER DE SCHAUENSEE, R. 1970. A guide to the birds of South America. Livingston Publ. Co., Wynnewood, Pennsylvania.

MOORE, R. T. 1934. The Mt. Sangay labyrinth and its fauna. Auk 51:141–156.

NEWTON, A. 1865. List of animals collected at Mohambo, Madagascar, by Mr. W. T. Gerrard. Proc. Zool. Soc. London 832–837.

PETERS, J. L. 1934. Check-list of birds of the world. Vol. 2. Harvard Univ. Press, Cambridge, Massachusetts.

PHELPS, W. H. AND W. H. PHELPS, JR. 1958. Lista de las aves de Venezuela con su distribución. Bol. Soc. Venezolena Cienc. Nat. 19, Tomo 2, Parte 1 (Num. 90).

PINTO, O. M. D. O. 1935. Aves de Bahia. Rev. Mus. Paulista 19:1–326.

POPHAM, H. L. 1898. Further notes on birds observed on the Yenesei River, Siberia. Ibis 10:489–520.

———. 1901. Supplementary notes on the birds of the Yenesei River. Ibis 13:449–458.

RAND, A. L. 1934. The distribution and habits of Madagascar birds. Bull. Am. Mus. Nat. Hist. 72:143–490.

REYNOLDS, P. W. 1935. Notes on the birds of Cape Horn. Ibis 77:65–101.

SEEBOHM, H. 1886. A review of the species of the genus *Scolopax*. Ibis 28:122–144.

STUBBS, F. J. 1912. Flight of the Common Snipe. Br. Birds 6:102.

SUTTON, G. M. 1923. Notes on the nesting of the Wilson's Snipe in Crawford County, Pennsylvania. Wilson Bull. 35:191–202.

———. 1928. The birds of Pymatuning Swamp and Conneaut Lake, northwestern Pennsylvania. Ann. Carnegie Mus. 18:19–239.

———. 1961. Iceland summer. Univ. Oklahoma Press, Norman, Oklahoma.

TERBORGH, J. AND J. S. WESKE. 1972. Rediscovery of the Imperial Snipe in Peru. Auk 89:497–505.

TUCK, L. M. 1972. The Snipes: a study of the genus *Capella*. Can. Wildl. Serv. Monogr. No. 5. Ottawa, Canada.

VAN SOMEREN, V. D. 1947. Field notes on some Madagascar birds. Ibis 89:235–267.

VUILLEUMIER, F. 1969. Field notes on some birds from the Bolivian Andes. Ibis 111:599–608.

WELTY, C. 1975. The life of birds, 2nd ed. Saunders, Philadelphia, Pennsylvania.

WETMORE, A. 1926. Observations on the birds of Argentina, Paraguay, Uruguay and Chile. U.S. Natl. Mus. Bull. 133.

WHITE, C. M. N. 1945. On the validity of *Capella angolensis* Bocage. Ibis 87:465–466.

WILLIAMSON, K. 1950. The distraction behaviour of the Faroe Snipe. Ibis 92:66–74.

WITHERBY, H. F., F. C. R. JOURDAIN, N. F. TICEHURST AND B. W. TUCKER. 1941. The handbook of British birds, Vol. 4. H. F. & G. Witherby Ltd., London, England.

WOLLEY, J. 1858. (Comments on W. Meves's paper [originally publ. in Swedish] on the Common Snipe's drumming.) Proc. Zool. Soc. London 199–202.

Woods, R. 1975. Birds of the Falkland Islands. Compton Press, Salisbury, Wiltshire, England.

STOVALL MUSEUM OF SCIENCE AND HISTORY, UNIV. OKLAHOMA, NORMAN, OKLAHOMA 73019. ACCEPTED 22 APR. 1981.

COLORPLATE

The colorplate Frontispiece of the Common Snipe (*Capella gallinago*) has been made possible by an endowment established by George Miksch Sutton.

ANNUAL MEETING—THE WILSON ORNITHOLOGICAL SOCIETY, 1982

The 63rd annual meeting of The Wilson Ornithological Society will be held at Virginia Polytechnic Institute and State University, Blacksburg, Virginia, 6–9 May, 1982. In addition to the scientific program, there will be an art exhibition and a program for spouses. Daily fieldtrips are planned for the Blacksburg area. On the morning of 9 May, there will be a fieldtrip to Mountain Lake, Virginia, elev. 4000+ feet, one hour distant from Blacksburg to see northern (boreal) breeding birds.

Chairman of the Local Committee is Dr. Curtis Adkisson, Dept. Biology, Virginia Polytechnic Institute and State University, Blacksburg, Virginia 24061. Information concerning accommodation, transportation and related matters will be mailed to the Society membership. Chairman of the Program Committee is Dr. Clait Braun, Wildlife Research Center, 317 W. Prospect St., Fort Collins, Colorado 80526. Abstracts of papers to be given in the scientific sessions must be received by him before 1 April 1982.

Wilson Bull., 93(4), 1981, pp. 478–490

FORAGING OF FIVE BIRD SPECIES IN TWO FORESTS WITH DIFFERENT VEGETATION STRUCTURE

Brian A. Maurer and Robert C. Whitmore

Specific foraging patterns of many bird species have been well studied; however, few studies have dealt with the influence of changes in habitat structure on foraging. This study examines the influence of vegetation structure on the foraging behavior of Acadian Flycatchers (*Empidonax virescens*), Red-eyed Vireos (*Vireo olivaceus*), Black-throated Green Warblers (*Dendroica virens*), American Redstarts (*Setophaga ruticilla*) and Scarlet Tanagers (*Piranga olivacea*). The foraging behavior of each of these species was observed in two habitats that had different vegetation structures. This made it possible to relate differences in foraging by the bird species to changes in habitat structure.

STUDY AREAS AND METHODS

Study areas.—Foraging data were gathered in two stands in the Fernow Experimental Forest (avg. elev. 760 m) located 4.8 km southeast of Parsons, Tucker Co., West Virginia. Major tree species in the Fernow Forest were red oak (*Quercus rubra*), chestnut oak (*Q. prinus*), red maple (*Acer rubrum*), sugar maple (*A. saccharum*), black cherry (*Prunus serotina*), American beech (*Fagus grandifolia*), yellow poplar (*Liriodendron tulipifera*) and sweet birch (*Betula lenta*). The relative abundances of these trees, however, varied between stands.

The Fernow Forest is in a region that is warm in summer. Maximum daily temperature was 30°C in 1977 and 29.4°C in 1978. Temperatures at night ranged from near 0°C in May to 16.1°C during July for both years. Weekly precipitation reached a maximum both years of >9 cm in the month of July. Precipitation dropped below 0.25 cm/week only one week during the 1977 season, and never dropped below 1 cm/week in 1978.

The two stands were located on watersheds that have been used for hydrological research by the Forest Service. One stand, the "young forest," (30 ha) was clearcut in 1958 and has since been left to regrow. In 1971 this area was fertilized using 257 kg/ha urea. The stand grows on very steep terrain, with about 75% of the slopes 21.8° or greater (Reinhart et al. 1963). The second stand, the "mature forest," (38.9 ha) was logged early in the 1900's, and has since been left to regrow. None of the slopes in this stand were steeper than 21.8°.

Avifauna.—The bird communities inhabiting the two stands represent an important context within which the species studied should be viewed. The species found in these communities included several species typical of northern coniferous forests, e.g., Blackburnian Warblers (*Dendroica fusca*), as well as species typical of deciduous forest habitats, e.g., Hooded Warblers (*Wilsonia citrina*). The young forest had fewer species of flycatchers, and had several species typical of early stages of forest succession, e.g., Chestnut-sided Warblers (*D. pensylvanica*) and Canada Warblers (*D. canadensis*). Cerulean (*D. cerulea*) and Blackburnian warblers occurred only in mature forest. Further information on the avian communities in these stands is given by McArthur (1980) and Maurer (1980).

Methods.—Both study areas were sampled in July 1978 for vegetation structure and composition. Fifty 0.04-ha circular plots were located randomly in each area. Vertical structural diversity was measured using frequency counts of vegetation in each of eight canopy layers

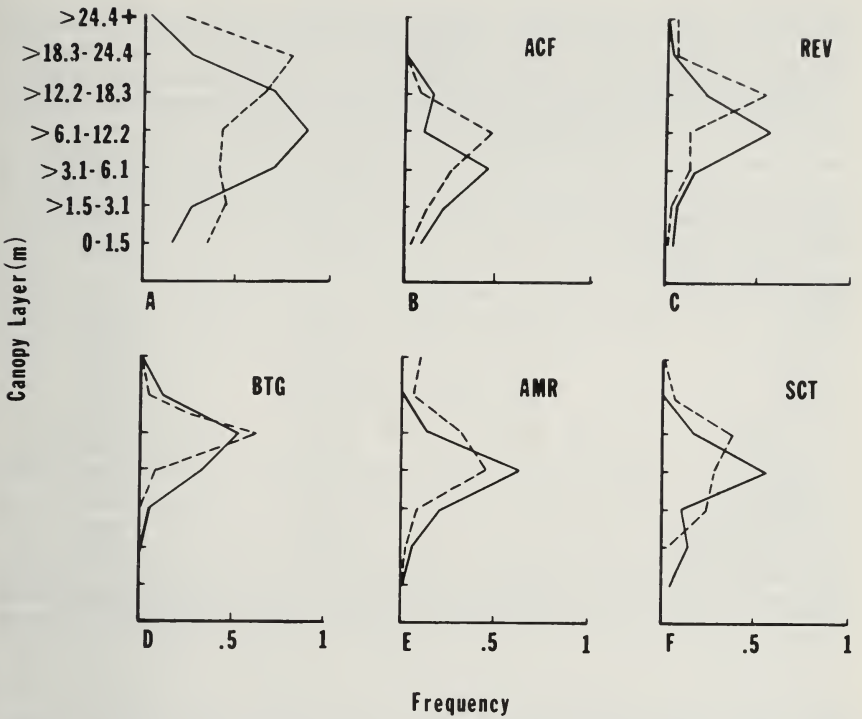


FIG. 1. Foliage height profile (A) and foraging height distribution (B–F) for five canopy-feeding birds in a mature forest (broken lines) and a young forest (solid lines). ACF = Acadian Flycatcher, REV = Red-eyed Vireo, BTG = Black-throated Green Warbler, AMR = American Redstart, SCT = Scarlet Tanager.

(low vegetation; shrubs: 0–1 m, 1.5–3.05; trees: 3.05–6.1, 6.1–12.2, 12.2–18.3, 18.3–24.4, >24.4) at 20 points within each plot and calculating a diversity index, $-\Sigma p_i \ln p_i$ (Pielou 1976), for each plot. Differences in plot diversities between areas were tested using a 2-sided Mann-Whitney test (Conover 1971). A profile of the canopy was obtained for each stand by using the frequency counts of vegetation in each of seven (excluding low vegetation) canopy layers (Fig. 1A). These profiles represent the probability of encountering a given canopy layer at any point in a study area. Probabilities were estimated from the samples taken in each area. Maximum canopy height was determined for each plot, and differences in canopy height between stands were tested using a 2-sided Mann-Whitney test. Relative densities (RD) were calculated for several tree species groups (Table 1) as follows: $RD = \Sigma A_i / \Sigma M_i$, where A_i = number of individuals of species group A in plot i and M_i = total number of trees in plot i.

Foraging behavior of five canopy feeding bird species were recorded from 8 May–27 July 1978 and 7 May–22 June 1979. Observations were classified into categories for each of four foraging variables. The variables (categories are in parentheses) were (1) foraging maneuver (hover, glean, flycatch), (2) foraging substrate (leaf, branch, trunk, air), (3) location in tree (proximal to the trunk, distal to the trunk, air), and (4) tree species used (*Quercus* spp., *Acer* spp., *Betula* spp., *Fagus* spp., other species, shrubs and saplings). Niche metrics (niche

Table 1

Vertical Diversity, Mean Canopy Height, Relative Densities and Tree Species Diversity of Two Stands in the Fernow Experimental Forest Based on 50 Random Plots Located in Each Stand

	Young forest	Mature forest
Mean vertical diversity	1.70	1.89
Mean canopy height (m)	20.31	24.53
Relative density (RD)		
Oaks	0.03	0.15
Maples	0.22	0.39
Beeches	0.06	0.12
Birches	0.07	0.07
Other (total)	0.62	0.26
Hickories	0.02	0.01
Cherries	0.02	0.06
Magnolias	0.16	0.16
Miscellaneous*	0.42	0.03
Tree species diversity	1.08	1.44

* White ash (*Fraxinus americana*), basswood (*Tilia* spp.), eastern hemlock (*Tsuga canadensis*), big-tooth aspen (*Populus grandidentata*), elms (*Ulmus*), service berry (*Amelanchier*), witch hazel (*Hamamelis virginia*), black locust (*Robinia pseudo-acacia*).

breadth, niche overlap) were calculated following Colwell and Futuyma (1971) for two niche dimensions: (1) foraging behavior and (2) tree use. The following nine independent foraging states were used to categorize the foraging data and calculate niche metrics related to foraging behavior: (1) hovering at foliage proximal to the trunk of a tree or shrub, (2) hovering at foliage distal to the trunk, (3) hovering at woody structures (branches, bark, etc.) proximal to the trunk, (4) hovering at woody structures distal to the trunk, (5) flycatching, (6) gleaning foliage proximal to the trunk, (7) gleaning foliage distal to the trunk, (8) gleaning woody structures proximal to the trunk, and (9) gleaning woody structures distal to the trunk. Niche metrics of the tree-use dimension were calculated using 13 independent resource states. These states were created using six tree species groups (*Quercus, Fagus, Acer, Betula,* other trees, shrubs) and dividing each of these groups into three groups based on the height of the foraging maneuver (0–3 m, 3–9 m, >9 m). Since the five species did not use some trees at certain heights, 13 instead of 18 resource states were used. Changes in niche widths between areas were tested using Hutcheson's (1970) method of testing for differences in diversity.

Heights of foraging acts were recorded for each species. From these data foraging heights were tested for significant differences between stands using a 1-sided Mann-Whitney test (Conover 1971). Foraging height profiles for each species were constructed for both forests. These profiles are analogous to the foliage height profiles described above and represent the estimated probabilities that any one foraging act by a given species in a given forest will be in a specific canopy layer.

Contingency tables were constructed (forest stand × foraging variable: maneuvers, substrates, locations, tree use) to test for differences in probabilities of each category between the two stands. Since multiple observations were obtained from some of the individuals of each species, the data might not represent a true random sample. This can cause the Chi-

square tests to produce liberal significance levels (E. J. Harner, pers. comm.). Thus, for the Chi-square tests, the significance level $P < 0.01$ was used. Tests for preferential use of tree species were performed using a Chi-square goodness of fit test. A hypothetical probability distribution was estimated from the relative densities for each tree species group (Table 1) in each stand. Using a Chi-square goodness of fit test (Conover 1971), the hypothesis that the probability distribution generated from relative densities of the tree species groups was the same as the probability distribution of foraging acts among the tree groups was tested for each bird species in each stand. For a given stand, a significant Chi-square value indicated that a bird species was deviating from a pattern of using tree species based on their abundance by selecting certain tree types over others. If a cell in any contingency table had an expected value <1, categories were lumped together to raise the value, thus reducing the degrees of freedom. When a cell in a contingency table has an expected value of <1, the significance level may be poorly approximated (Conover 1971).

HABITAT STRUCTURE

Canopy structure was more diverse (Mann-Whitney $U = 195$, $P < 0.001$) in the mature forest than the young forest (Table 1). This means that, on the average, a point in the mature forest had more canopy layers than a point in the young forest. The trend of greater complexity in the mature forest was reflected in the vertical profile of that forest (Fig. 1A). The mature forest also had a higher (Mann-Whitney $U = 358$, $P < 0.001$) mean canopy height (Table 1) than the young forest. The frequencies of each canopy layer were significantly different in each stand ($\chi^2 = 867.3$, df = 6, $P < 0.001$). In the mature forest, the most abundant canopy layer was at 18.3–24.4 m (Fig. 1A). Layers below the 18.3–24.4 m layer were well represented in that forest. In the young forest, there was a high incidence of three layers (3.1–6.1 m, 6.1–12.2 m, 12.2–18.3 m), but the rest of the layers were poorly represented.

FORAGING BEHAVIOR

Acadian Flycatcher.—Acadian Flycatchers used essentially the same foraging maneuvers in both forests ($\chi^2 = 0.09$, df = 1, NS). Hovering at various substrates was used most often, while gleaning was rarely used (Table 2). The use of locations (proximity to trunk) ($\chi^2 = 7.28$, df = 2, $P = 0.027$), and the use of substrates ($\chi^2 = 13.20$, df = 3, $P = 0.005$) were different. Woody structures (e.g., branches) were used as foraging sites in the young forest but not in the mature forest.

Acadian Flycatchers also showed significantly different patterns of tree use in both forests ($\chi^2 = 20.90$, df = 5, $P = 0.001$). Shrubs and trees other than maples, beeches, birches and oaks were used more often in the young forest than in the mature forest (Table 3). Acadian Flycatchers did not use tree types based on their abundance in the young forest ($\chi^2 = 36.77$, df = 4, $P < 0.001$) or the mature forest ($\chi^2 = 23.51$, df = 4, $P < 0.001$). In both habitats, beeches were used more often than expected by chance

TABLE 2
RELATIVE FREQUENCIES OF FORAGING VARIABLES FOR FIVE SPECIES OF INSECTIVOROUS BIRDS

Species	No. of observations	Maneuver			Location[a]		Substrate[a]		
		Hover	Glean	Hawk	Prox[b]	Dist	Leaf	Branch	Trunk
E. virescens									
Young forest	72	59.7	1.4	38.9	19.4	40.3	40.3	5.6	15.3
Mature forest	53	58.5	0.0	41.5	3.8	54.7	58.5	0.0	0.0
V. olivaceus									
Young forest	59	52.5	47.5	0.0	8.5	91.5	81.4	15.4	3.4
Mature forest	48	52.1	47.9	0.0	6.3	93.8	91.7	4.2	4.2
D. virens									
Young forest	31	45.2	38.7	16.1	0.0	83.9	61.3	22.5	0.0
Mature forest	30	43.3	30.0	26.7	23.3	50.0	43.3	23.3	6.7
S. ruticilla									
Young forest	71	54.9	7.0	38.0	11.3	50.7	52.1	7.0	4.2
Mature forest	47	34.0	10.6	55.3	6.4	38.3	23.4	19.1	2.1
P. olivacea									
Young forest	35	74.3	25.7	0.0	17.1	82.9	74.3	11.4	14.3
Mature forest	31	67.7	32.3	0.0	12.9	87.1	83.9	16.1	0.0

[a] Air same frequency as hawk (=flycatch).
[b] Prox = proximal to trunk, Dist = distal to trunk.

(cell χ^2 for beeches made up 84% of the χ^2 value for young forest, 64% for mature forest). Smith (1977) found that Acadian Flycatchers tend to use mesic sites, and since beeches are often associated with mesic sites (Fowells 1965, Brockman 1968) the association between beeches and this flycatcher is not unexpected.

Probabilities of using each canopy layer were different ($\chi^2 = 21.26$, df = 4, $P < 0.001$) in each study area (Fig. 1B). In both forests, Acadian Flycatchers concentrated their foraging efforts below the densest part of the canopy (Fig. 1A), as Williamson (1971) also noted. Foraging heights were lowest in the young forest (Table 3).

Acadian Flycatchers had a significantly wider foraging behavior niche in the young forest ($t = 4.77$, df = 124, $P < 0.005$) than in the mature forest. However, tree use was significantly more diverse in the mature forest ($t = 2.35$, df = 125, $P < 0.025$). The wider foraging niche was apparently due to increased use of different substrates (Table 2). In the young forest, Acadian Flycatchers had higher average overlaps with other species in foraging behaviors (Table 4), a pattern observed for other

TABLE 3
RELATIVE FREQUENCIES OF TREE SPECIES USE AND FORAGING HEIGHTS OF FIVE SPECIES OF FOREST BIRDS

Species	Tree use						Mean foraging height (m)	P^*
	Maple	Oak	Birch	Beech	Other	Shrub		
E. virescens								
Young forest	18.1	0.0	2.8	16.7	26.4	36.1	5.18	<0.01
Mature forest	26.4	9.4	11.3	26.4	7.5	18.9	8.09	
V. olivaceus								
Young forest	39.0	11.9	8.5	15.3	16.9	8.5	9.96	0.09
Mature forest	22.9	16.7	12.5	12.5	20.8	14.6	13.31	
D. virens								
Young forest	12.9	12.9	32.3	16.1	22.5	3.2	13.83	<0.01
Mature forest	13.3	20.0	23.3	23.3	20.0	0.0	18.72	
S. ruticilla								
Young forest	40.8	0.0	11.3	22.5	21.1	4.2	9.53	0.10
Mature forest	51.1	19.1	8.5	12.8	4.3	4.3	11.43	
P. olivacea								
Young forest	31.4	34.3	2.9	0.0	17.1	14.3	9.23	>0.10
Mature forest	38.7	6.5	0.0	32.3	12.9	9.7	11.87	

* Significance level from 1-sided Mann-Whitney test (Conover 1971) for differences in foraging heights between the two stands.

species. However, patterns of overlap with individual species varied (Maurer 1980). There was less average overlap between Acadian Flycatchers and other species in tree use in the young forest (Table 4).

Red-eyed Vireo.—Red-eyed Vireos did not show any significant differences in foraging or tree use between the two forests (critical levels for all tests were >0.05). Frequencies of foraging maneuvers, foraging locations and substrates used were very similar, although there was a slightly greater use of branches in the young forest (Table 2). The data indicate that these birds foraged mainly on foliage at the outer perimeter of a tree, hovering and gleaning about equally, as reported previously by James (1976) for southern Ontario and Williamson (1971) for Maryland.

Red-eyed Vireos did not change tree use between areas, but foraged slightly higher in the mature forest (Table 3). Probabilities of foraging in each canopy layer were different between stands ($\chi^2 = 29.33$, df = 6, $P < 0.001$). In the mature forest, the 12.2–18.3 m canopy layer was used most often, whereas the 6.1–12.2 m layer was used most often in the young

TABLE 4
NICHE DIMENSIONS OF FIVE CANOPY-FEEDING BIRDS IN TWO STRUCTURALLY DIFFERENT FORESTS

	Niche width (bits)				Average overlap (%)			
	Foraging		Tree use		Foraging		Tree use	
Species	Y[a]	M	Y	M	Y	M	Y	M
E. virescens	1.33	0.82	1.85	2.13	0.60	0.55	0.38	0.55
V. olivaceus	1.39	1.09	2.07	1.91	0.61	0.47	0.57	0.64
D. virens	1.47	2.01	1.63	1.59	0.64	0.51	0.44	0.53
S. ruticilla	1.30	1.30	1.85	1.66	0.64	0.47	0.50	0.60
P. olivacea	1.26	1.21	1.85	1.74	0.61	0.52	0.43	0.54
$\bar{x}$ =	1.35	1.28	1.85	1.81	0.62	0.50	0.46	0.57
Significance[b]	NS		NS		$P < 0.025$		$P < 0.01$	

[a] Y = young forest, M = mature forest.
[b] Niche widths tested using d-test of Crow et al. (1978); overlaps tested using paired *t*-tests, df = 9.

forest (Fig. 1C). Lower foraging heights in the young forest were related to lower canopy height of that forest (Table 1, Fig. 1A).

Red-eyed Vireos in the young forest had wider niche widths for foraging behaviors (Table 4), although this difference was not statistically significant ($t = 1.89$, df = 3634, NS). The slightly wider niche in the young forest is due to the slight increase in use of branches in that forest (Table 2). Red-eyed Vireos also had a slightly wider tree-use niche in the young forest (Table 4), although again the difference was not statistically significant ($t = 1.50$, df = 102, NS). This suggests relative similarity in tree use between the two forests. In the young forest, tree use was not based on abundance ($\chi^2 = 53.38$, df = 4, $P < 0.001$), but was in the mature forest ($\chi^2 = 5.81$, df = 4, NS). In the young forest, a preference for mature forest types was shown. Niche overlaps of Red-eyed Vireos with other species for foraging were generally higher in the young forest, with the exception of Acadian Flycatchers. For tree use, niche overlaps were generally higher in the mature forest, except for overlap with American Redstarts, where tree-use overlap was higher in the young forest (Maurer 1980).

In summary, Red-eyed Vireos showed little reaction to foliage changes in their foraging behavior, except for foraging higher in the stand with a higher canopy. A slight broadening of their niche may occur in young forest, and relationships (overlaps) with other species change. Changes in relationships with other species were due to foraging shifts by other species rather than foraging changes by Red-eyed Vireos.

Black-throated Green Warbler.—Black-throated Green Warblers showed

few changes in foraging between areas, except that they foraged in different locations ($\chi^2 = 7.94$, df = 1, $P = 0.005$). In the mature forest, warblers used the inner parts of branches and trunks, while neither of these locations were used in the young forest (Table 2). Such limited changes in foraging behavior were noticed in other studies conducted in spruce forests (MacArthur 1958; Morse 1968, 1971; Rabenold 1978). Foraging heights were higher in the mature forest than in the young forest (Table 3), although probabilities of foraging in each canopy layer were not different ($\chi^2 = 9.77$, df = 4, $P = 0.046$). In the young forest, Black-throated Green Warblers used a greater variety of foraging heights.

Black-throated Green Warblers had a wider foraging niche in the mature forest than in the young forest (Table 4; $t = 3.78$, df = 58, $P \leq 0.001$). Tree-use niches were of similar width in both forests (Table 4, $t = 0.53$, df = 39, $P > 0.1$). As opposed to foraging behaviors, tree use by Black-throated Green Warblers was narrower than other species.

As with other species, foraging overlaps were highest for Black-throated Green Warblers in the young forest, while tree-use dimension overlaps were lowest for all species in that forest (Table 4). Contrary to the pattern, foraging overlaps were higher with American Redstarts in the mature forest (Maurer 1980) because both species did more flycatching in the mature forest (Table 2).

American Redstart.—American Redstarts changed maneuvers ($\chi^2 = 9.47$, df = 2, $P = 0.009$) in the two forests; however, no differences in foraging locations were detected ($\chi^2 = 3.56$, df = 2, $P = 0.24$). The redstart was the only species that changed its foraging maneuvers between forests. Ficken (1962) noted that this species was very versatile in its use of foraging behaviors. The change in maneuvers was probably due to the greater amount of flycatching done in the mature forest, coupled with less hovering. In the young forest, there was a concentration of foraging (mainly hovering) on leaves (Table 2).

Redstarts used different tree species in each forest ($\chi^2 = 16.67$, df = 4, $P = 0.003$). Foraging was concentrated on maples and oaks in the mature forest, while oaks were not used at all in the young forest (Table 3). Use of tree types was independent of their abundance in the young forest ($\chi^2 = 69.74$, df = 4, $P < 0.001$) and the mature forest ($\chi^2 = 11.46$, df = 4, $P = 0.023$). Generally, maples were used more often than expected by chance.

Redstarts foraged significantly higher in the mature forest (Table 3). The distribution of foraging acts (Fig. 1E) among canopy layers was different in each forest ($\chi^2 = 19.11$, df = 5, $P < 0.005$). In the young forest, redstarts foraged heavily in the 6.1–12.2 m canopy layer, the densest layer in that forest. In contrast, redstarts in the mature forest spent more time

foraging in higher canopy layers, less time in lower layers and foraging in the 6.1–12.2 m canopy layer was less pronounced.

Widths of foraging niches were not statistically different ($t = 0.15$, df = 104, NS) between stands (Table 4). Tree-use niches were not significantly different ($t = 1.64$, df = 103, $P > 0.1$), indicating that the same pattern observed for foraging was present in tree use. That is, redstarts were highly opportunistic in their use of maneuvers and tree species, though this was not reflected in niche breadths. Foraging overlaps were greater in the young forest for redstarts and tree-use overlaps were lower in that forest (Table 4).

Scarlet Tanager.—This species did not show any differences in foraging behavior between stands (critical levels for maneuvers, substrates and locations all >0.01). Hovering at leaves was the foraging technique used most often (Table 2), more so than for any other species. Although no foraging changes occurred, Scarlet Tanagers did show differences in tree use between forests ($\chi^2 = 26.48$, df = 3, $P < 0.001$). Oaks were used more often in the young forest, while beeches were used more often in the mature forest (Table 3).

Scarlet Tanagers foraged at the same heights in both forests (Table 3). No difference in the distribution of foraging acts among canopy layers (Fig. 1F) was detected ($\chi^2 = 9.47$, df = 45, NS).

Niche widths were not different between forests for foraging ($t = 0.29$, df = 66, NS) and tree use ($t = 1.07$, df = 45, NS). Scarlet Tanagers showed the same patterns for overlaps that other species did (Table 4). Contrary to the pattern, there was higher tree-use overlap with Black-throated Green Warblers in the young forest (Maurer 1980).

The changes these five bird species demonstrated are summarized in Table 5.

DISCUSSION

Differences in habitat structure between the two stands affected some of the species more than others (Table 5). The amount of foraging changes demonstrated by a species was related to the amount of flycatching that a species did. The two species which did not flycatch, Red-eyed Vireos and Scarlet Tanagers, showed few changes in their foraging patterns between areas. Acadian Flycatchers and American Redstarts, which had the highest frequencies of flycatching, showed the most changes in foraging (Table 5), while Black-throated Green Warblers were intermediate in both amount of flycatching and number of foraging changes. These data suggest that flycatching species tend to be more opportunistic when presented with different foraging opportunities than non-flycatching species.

TABLE 5

CHANGES IN FORAGING STRATEGIES OF FIVE SPECIES OF INSECTIVOROUS BIRDS[a]

Species	Foraging behavior		Tree use	Foraging heights	Niche width
	Manuevers	Locations and substrates			
E. virescens	no changes	decreased use of woody substrates, increase in use of peripheral foliage	increased use of oaks, maples, beeches, decreased use of shrubs	higher	narrower foraging, wider tree use
V. olivaceus	no changes	no changes	no changes	slightly higher	no changes
D. virens	no changes	decreased use of peripheral foliage	no changes	higher	wider foraging, no change in tree use
S. ruticilla	more flycatching	less use of foliage	increased use of maples	slightly higher	no changes
P. olivacea	no changes	no changes	decreased use of oaks, increased use of beeches	no change	no changes

[a] Changes are those that occur in the mature forest relative to the young forest.

The major structural difference between the two forests was an increased amount of open area beneath the main concentration of leaves in the mature forest. Acadian Flycatchers had narrower foraging niches in that forest. Since this species foraged mainly in these open areas beneath the canopy, the increase of open areas in the mature forest suggests more resources were available to the flycatchers. The narrower foraging niche of this species is consistent with the predictions of several optimal resource use models (MacArthur 1972, Pyke et al. 1977). Two other species also appeared to react to the increased open spaces in the mature forest. Black-throated Green Warblers broadened their foraging niche in the mature forest by flycatching more often. Redstarts switched from hovering most often in the young forest to flycatching most often in the mature forest. These last two species reacted opportunistically to an increase in a potential resource by altering their use of foraging techniques to reflect the increase in the resource.

Parallel changes in foraging between forests, such as those discussed in the preceding paragraph, suggest, at least for the species considered, that competition was not a proximate cause of foraging shifts. Similar parallel changes in foraging heights were demonstrated by Red-eyed Vireos, American Redstarts and Scarlet Tanagers. Each of these species concentrated foraging behaviors in the dense 6.1–12.2 m canopy layer in the young forest which again seemed to suggest changes were occurring in response to greater abundance of a potential resource. The results of this study clearly demonstrate that bird species do modify their foraging behavior when presented with altered resource distributions due in part to changes in the structure of the habitat (see Grubb 1979). If species respond opportunistically to changes in resource levels, what role would such opportunism play in determining which species were present in a given habitat? Further, which is more important in determining community structure, the species' own abilities to use resources in a given habitat or the number of competitors using that resource? This study implies that the answer to these questions may be different than the "classical" answers (e.g., Cody 1974). Further research is needed to clarify the relationship between individual species' foraging patterns and patterns of community structure. Holmes et al. (1979) did a community wide study of foraging behavior and concluded that the structure and composition of the plant community played a major role in determining bird community structure within and between habitats. The results of our study are very much in agreement with this idea, and suggest to us that changes in bird communities between habitats are related to altered resource distributions resulting from changes in the structure and species makeup of the plant community.

SUMMARY

The influence of habitat structure on the foraging behavior of five bird species was studied in two stands in the Fernow Experimental Forest. Vegetation structure of the stands was found to be different. One stand had a high, stratified canopy with a well-developed understory and the other had a lower, less stratified, but denser canopy without a well-developed understory. Each bird species showed differences in foraging behaviors that could be related to differences in vegetation structure. One species, American Redstart, changed foraging maneuvers between forests. Changes by other species involved use of different substrates or locations in trees, use of different tree species, or changes in foraging heights. Species that foraged by gleaning and hovering at foliage demonstrated different foraging behaviors less often than species which foraged by flycatching. Some species in this study showed changes in their foraging that coincided with increases in potential resources, e.g., Acadian Flycatchers did more flycatching in the forest with more open subcanopy area. Parallel changes in several instances suggested that competition was not a proximate cause of these changes.

ACKNOWLEDGMENTS

We thank G. E. Lang, E. J. Harner, R. F. Johnston and J. Rice for reading a previous draft of this manuscript and offering many valuable suggestions. E. J. Harner provided a great deal of assistance with statistical methods. We thank the Timber and Watershed Laboratory, U.S.D.A. Forest Service, at Parsons, West Virginia for providing housing. Funding for this research was provided by McIntire-Stennis Project #17. This research was done in partial fulfillment of the requirements for an M.Sc. degree by the senior author with the Division of Forestry, West Virginia University. Published with the approval of the Director, West Virginia University Agricultural and Forestry Experiment Station as scientific article 1728.

LITERATURE CITED

Brockman, C. F. 1968. Trees of North America. Golden Press, New York, New York.

Cody, M. L. 1974. Competition and the structure of bird communities. Princeton Univ. Press, Princeton, New Jersey.

Colwell, R. K. and D. J. Futuyma. 1971. On the measurement of niche breadth and overlap. Ecology 52:567–576.

Conover, W. J. 1971. Practical nonparametric statistics. John Wiley and Sons, New York, New York.

Crow, E. L., F. A. Davis and M. W. Maxfield. 1978. Statistics. Coles Publishing, Toronto, Ontario.

Ficken, M. S. 1962. Maintenance activities of the American Redstart. Wilson Bull. 74:153–165.

Fowells, H. A. 1965. Silvics of forest trees of the United States. USDA For. Serv. Agric. Handbook No. 271.

Grubb, T. C. 1979. Factors controlling foraging strategies of insectivorous birds. Pp. 119–135 *in* The role of insectivorous birds in forest ecosystems (J. G. Dickson, R. N. Connor, R. R. Fleet, J. A. Jackson and J. C. Kroll, eds.). Academic Press, New York, New York.

Holmes, R. T., R. E. Bonney, Jr. and S. W. Pacala. 1979. Guild structure of the Hubbard Brook bird community: a multivariate approach. Ecology 60:512–520.

Hutcheson, K. 1970. A test for comparing diversities based on the Shannon formula. J. Theor. Biol. 29:151–154.

James, R. D. 1976. Foraging behavior and habitat selection of three species of vireos in southern Ontario. Wilson Bull. 88:62–75.

MacArthur, R. H. 1958. Population ecology of some warblers of northeastern coniferous forests. Ecology 39:599–619.

———. 1972. Geographical ecology. Harper and Row, New York, New York.

Maurer, B. A. 1980. Avian foraging and habitat structure in an eastern deciduous forest in West Virginia. M.Sc. thesis, West Virginia Univ., Morgantown, West Virginia.

McArthur, L. B. 1980. The impact of various forest management practices on passerine community structure. Ph.D. diss., West Virginia Univ., Morgantown, West Virginia.

Morse, D. H. 1968. A quantitative study of foraging of male and female spruce-woods warblers. Ecology 49:779–784.

———. 1971. The foraging of warblers isolated on small islands. Ecology 52:216–228.

Pielou, E. C. 1976. Mathematical ecology. John Wiley and Sons, New York, New York.

Pyke, G. H., H. R. Pulliam and E. L. Charnov. 1977. Optimal foraging: a selective review of theory and tests. Quart. Rev. Biol. 52:137–154.

Rabenold, K. N. 1978. Foraging strategies, diversity and seasonality in bird communities of Appalachian spruce-fir forests. Ecol. Monogr. 48:397–424.

Reinhart, R. G., A. R. Eschner and G. R. Trimble. 1963. Effect on streamflow of four forest practices in the mountains of West Virginia. Upper Darby, Pennsylvania, Northeast For. Exper. Stat., USDA For. Serv. Res. Pap. NE–1.

Smith, K. G. 1977. Distribution of summer birds along a forest moisture gradient in an Ozark watershed. Ecology 58:810–819.

Williamson, P. 1971. Feeding ecology of the Red-eyed Vireo (*Vireo olivaceus*) and associated foliage-gleaning birds. Ecol. Monogr. 41:129–152.

Div. Forestry, West Virginia Univ., Morgantown, West Virginia 26506. (Present address BAM: Center for Quantitative Studies, Coll. Agriculture, Univ. Arizona, Tucson, Arizona 85721.) Accepted 12 Mar. 1981.

Wilson Bull., 93(4), 1981, pp. 491–499

AGE AND SEX DIFFERENCES IN WING LOADING AND OTHER AERODYNAMIC CHARACTERISTICS OF SHARP-SHINNED HAWKS

Helmut C. Mueller, Daniel D. Berger and George Allez

Wing area, wing loading and other aerodynamic characteristics are particularly important for the diurnal raptors, birds that spend considerable time on the wing or rely on agility in flight for the capture of prey. Brown and Amadon (1968) summarize data available on wing loading for various Falconiformes and list measurements for only 56 species. Of these 56, exactly half of the wing loadings are based on a sample of only one, both sexes were measured for only seven species and age was not noted for any. In this paper we examine age and sex differences in wing area, wing loading and other aerodynamic characteristics of Sharp-shinned Hawks (*Accipiter striatus*) based on a sample of 255 wings and 108 tails. The hawks were captured in a variety of traps (see Bub 1974) at the Cedar Grove Ornithological Station, on the western shore of Lake Michigan near Cedar Grove, Sheboygan Co., Wisconsin. A description of the Cedar Grove region can be found in Mueller and Berger (1966) and an account of the migrations of sharp-shins is given in Mueller and Berger (1967).

TECHNIQUES

Birds were measured on the day they were captured. Wing chord was measured by placing the wrist (bend) of the wing at the zero point of a rule and pivoting the folded wing downward until the tip of the longest primary just touched the rule. Tail length was measured by inserting a thin metal rule between the central rectrices and sighting across the tops of the longest rectrices of the folded tail. Both linear measurements were taken to the nearest mm. Birds were weighed to the nearest gram on a balance graduated in 0.1 g increments. Esophageal ("crop") contents, if any, were estimated and subtracted from the gross weight.

The right wing of a hawk was photographed while the ventral side was held against a vertical, rigid sheet of clear plastic ruled into 5 cm squares (Fig. 1). In addition to the squares a 10 × 30 cm rectangle was outlined in fine black tape. A white window shade about 1 m behind the plastic provided contrast. The body of the hawk was held with one hand against the edge of the plastic and the wing was held by the manus with the other hand so that the wing was barely in contact with the plastic. Another person photographed the wing, stationing himself normal to the wing. The date, age, sex and band number of the hawk were affixed to the plastic and included in the photograph.

The negatives of the wing photographs were mounted in slide holders and projected to life size using a projector with a zoom lens and matching the 10 × 30 cm rectangle with one drawn on the screen. The outline of the wing was traced on a piece of paper, along with an estimated half width of the body. In some photographs the wing was pulled away from the body, exposing the axillars. The axillars were not included in the measurement of wing area. The tracing was measured to the nearest 0.1 cm^2 with a compensating polar planimeter.

FIG. 1. Photograph of spread of wing of a Sharp-shinned Hawk.

Each tracing was measured twice, or until 2 measurements were obtained that differed by less than 1%. In a test of the accuracy of wing measurement the wing of 1 hawk was photographed 15 times. Holders and photographers were alternated quasi-randomly among the three authors. Each of us held the bird 5 times. Between photographs, the bird was returned to its holding tube for at least a few minutes. An analysis of variance revealed no significant difference among holders. The area for the right wing was 272.43 ± 10.18 (SD), yielding a standard error of measurement of 2.07% at the 95% confidence interval.

On the tracing, wing length was measured from the tip of the longest primary to the body. Wing span was obtained by adding wing length to the measurement of half body width and multiplying by 2. Average wing width was calculated by dividing the area of one wing by wing length. Aspect ratio was obtained by dividing wing length by wing width. The wing area given in Table 1 was obtained by multiplying the area of the measured wing by 2. Wing load was calculated by dividing the weight of the bird by its total wing area.

Holding the tail of a live bird for photographing the area is difficult. Tails were held up against the vertical plastic used for wing measurements (Fig. 2). Angles of spread varied from 41°–111°. Photographic negatives were projected and traced using the same methods as for wings. The base of the tail was obscured by the holder, and we resorted to the following adjustments. A straight edge was oriented along the outer edge of the outermost rectrix on the tracing and a line drawn extending the base of the tail (dashed lines in Fig. 3). This procedure was repeated for the other side of the tail so that the two extended lines met. The angle thus formed (A) was measured as the angle of spread. The distance from the apex of

TABLE 1

WING AREA AND RELATED MEASUREMENTS FOR SHARP-SHINNED HAWKS

Measurements	Adult ♂♂ N = 54 $\bar{x}$ ± SD	Juvenile ♂♂ N = 90 $\bar{x}$ ± SD	Adult ♀♀ N = 54 $\bar{x}$ ± SD	Juvenile ♀♀ N = 57 $\bar{x}$ ± SD
Wing chord (cm)	17.24 ± 0.33**[a]	16.88 ± 0.32	20.22 ± 0.78**	19.92 ± 0.35
(corrected)	(17.15)**	(16.87)		
Wing length (cm)	24.35 ± 0.72**	23.77 ± 1.02	28.52 ± 1.10**	27.75 ± 0.73
Wing width (cm)	8.91 ± 0.31*	8.83 ± 0.24	10.33 ± 0.44*	10.20 ± 0.30
Wing span (cm)	53.06 ± 1.45**	51.98 ± 2.06	64.02 ± 2.18*	62.21 ± 1.47
Aspect ratio	2.74 ± 0.12**	2.69 ± 0.11	2.76 ± 0.13*	2.72 ± 0.09
Wing area (cm^2)	434.06 ± 20.78**	419.93 ± 25.78	589.77 ± 38.85**	565.29 ± 24.84
(corrected)	(429.94)*	(420.63)		
Weight (g)	101.24 ± 6.42**	96.43 ± 5.97	176.26 ± 11.57**	163.38 ± 9.03
(corrected)	(102.89)**	(97.50)		
Wing load (g/cm^2)	0.233 ± 0.02	0.230 ± 0.02	0.300 ± 0.03**	0.289 ± 0.02
(corrected)	(0.239)**	(0.232)		

* Differs significantly from juveniles, $P < 0.05$, *t*-test, 1-tailed; ** differs significantly from the juveniles, $P < 0.01$.
[a] Significantly larger than the mean given in Mueller et al. (1979), $P < 0.05$, *t*-test, 2-tailed. Corrected means for wing chord and weight are from the larger sample of Mueller et al., (1979). Corrected wing areas are based on regressions of area on wing chord.

this angle to the longest rectrices was measured (B), and from this measurement we subtracted tail length (D, as measured from the live bird). This difference (C) was then measured from the apex of the angle and an arc drawn across the tail with a compass (dashed line). The tail area measured with the planimeter included everything within solid and dashed lines except the basal segment of the circle with radius C (Fig. 3). Since tail area varies with angle of spread, we developed a formula which estimates tail area. We first calculated for each tail: (sin A)(length^2), where A is the angle of spread and length is the tail length measured from the live bird. We then calculated a linear regression for all 108 tails, giving us the formula:

$$\text{Area} = 4.1189 + 0.9624(\sin A[\text{length}^2]).$$

The equation is an excellent fit to the data ($r = 0.98$).

RESULTS

Wing photographs were taken when sufficient personnel were available, and the sample of 255 wing area photographs was not randomly distributed throughout the autumn. We have found that the population of Sharp-shinned Hawks caught at Cedar Grove shows complex changes in wing chord and weight through the autumn (Allez et al., unpubl.), and the birds sampled for wing areas thus might not be representative. We compared wing chord and weight from our sample for wing areas with wing chord and weight from a sample of almost 2000 birds taken from the entire season in the years 1953–1964 (Mueller et al. 1979).

FIG. 2. Photograph of spread of tail of a Sharp-shinned Hawk.

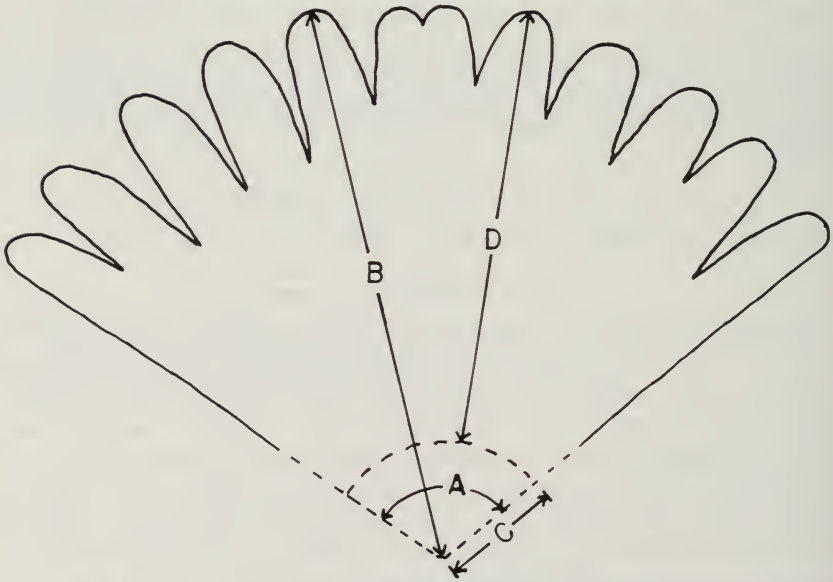


FIG. 3. Method of measuring tail area. The solid lines are traced from Fig. 2. See text for explanation of dashed lines and symbols.

Only one measurement from the sample wing areas differed significantly (t-test, $P < 0.05$, 2-tailed) from those of the larger sample—adult males had significantly longer wing chords in the sample taken for wing area. In addition, these adult males were almost significantly lighter in weight ($P < 0.08$). Since wing area is in part a function of wing length, our sample of wing areas for adult males thus overestimates wing area and underestimates wing loading. To obtain better estimates, we performed linear regressions of wing chord on wing area for both adult and juvenile males and then calculated "corrected" wing areas and wing loadings based on the mean wing chords and weights from the larger sample of Mueller et al. (1979).

Adults of both sexes are significantly larger than juveniles in all measurements: wing chord, wing length, wing width, wing span, aspect ratio, wing area, weight and wing loading; with one exception—the wing loading of males (Table 1). However, the corrected estimates of wing loading of males, based on the larger, more representative sample, show a significantly greater wing loading for adults than juveniles, as well as significantly greater wing chord, wing area and weight. Two differences between adults and juveniles are disproportionate: (1) the increase in width of wings in adults is less than half the increase in wing length, resulting in a higher aspect ratio in adults, and (2) the increase in wing area in adults is proportionately only about half as great as the increase in weight resulting in higher wing loading in adults. Females of both age groups are significantly larger than males ($P < 0.0001$) in wing chord, wing length, wing width, wing span, wing area, weight and wing loading but do not differ significantly in aspect ratio ($P > 0.05$, Table 1).

Estimated tail areas for three angles of spread are presented in Table 2. The tail lengths used to calculate areas using the regression equation are the means from Mueller et al. (1979) because three of the four means from the samples taken from tail photographs differed significantly from the means from the larger sample. We have examined spread tails in many live Sharp-shinned Hawks, a few dead individuals and the 102 photographs for tracings; in all of these, of course, the tail was spread manually by us. We estimate that a Sharp-shinned Hawk in normal flapping flight has its tail spread about 15°. We estimate that the maximum possible spread, without separation of rectrices, is about 100°. The tail shown in Figs. 2 and 3 is spread 107°. At 120° of spread there is some separation of rectrices, and the areas presented for this angle of spread probably are overestimates. In Table 2 we also present total flight surface area (wings plus tail) and the loading of total flight surface. The tail areas of juveniles average about 3% greater than that of adults. The total flight surface area of adults is greater because adults have greater wing areas than juveniles (Table 1). Tail area constitutes only about 10% of the total flight surface

TABLE 2
ESTIMATED TAIL AREAS IN SHARP-SHINNED HAWKS

Age	Sex	Area (cm^2)	Total surface[a]	Load[b] (g/cm^2)
		Tail spread 15°		
Adult	♂	47.75	477.69	0.215
Juvenile	♂	49.17	469.80	0.208
Adult	♀	64.50	654.27	0.269
Juvenile	♀	66.03	631.32	0.259
		Tail spread 100°		
Adult	♂	201.97	631.91	0.163
Juvenile	♂	208.39	629.02	0.155
Adult	♀	277.94	867.71	0.203
Juvenile	♀	284.84	850.13	0.192
		Tail spread 120°		
Adult	♂	256.99	686.93	0.150
Juvenile	♂	265.19	685.82	0.142
Adult	♀	354.08	943.85	0.187
Juvenile	♀	362.90	928.15	0.176

[a] Wing and tail area.
[b] Total surface load.

area when the tail is spread 15°, but when the tail is spread 100° the tail constitutes about a third of the total flight surface area. The difference between adults and juveniles in total flight surface area is about 1.7% (males) to 3.6% (females) when the tail is spread 15°. This difference decreases to 0.5% and 2.1%, respectively, when the tail is spread 100°.

The total surface loading is about 3.5% greater in adults when the tail is spread 15°; this difference increases to about 5.5% when the tail is spread 100°. Juveniles thus have considerably lower flight-surface loadings when the tail is spread.

DISCUSSION

Adults are larger than juveniles in every measurement taken except tail length and tail area; adults are larger than juveniles in many animals but in birds the restrictions imposed by flight and the persistence of non-growing remiges and rectrices for a year or longer impose severe limits on the magnitude of age differences. Birds cannot gradually increase in size; the change is rapid as old flight feathers are replaced by new. A large change in the length of remiges would require compensatory large and rapid changes in musculature and perhaps even in the skeleton or in large

changes in flight and foraging behavior. Mueller and Berger (1970) have shown that sharp-shins require considerable experience to perfect predatory techniques; rapid transitions in these behaviors are unlikely. The differences in size between adult and juvenile Sharp-shinned Hawks are small, but are statistically significant, and we believe that there is an adaptive rationale for these differences.

A bird is able to fly because an airfoil moving through the air generates lift. A bird moving through the air also induces drag, turbulent eddies which reduce its speed. Much of the induced drag is generated by vortices at the tip of the wing. In gliding flight, aerodynamic efficiency is maximized by increasing the aspect ratio of the wing (length/width), in effect decreasing the portion of the total wing area which is at the tip where lift is diminished by induced drag. In flapping flight a long wing is less "efficient" because it requires more power to move a long wing than a short one. A gliding bird has a minimum (stalling) speed. Flight is impossible at slower speeds because the airflow over the wings breaks up into turbulent eddies and lift is lost. Stalling speeds are a function of wing loading (the weight carried by the wing area). High wing loadings produce high stalling speeds and low wing loadings permit birds to fly more slowly. A bird can maintain flight speed by decreasing its angle of attack (the angle the wing makes with the horizontal), and thus losing altitude, or by powered flight (flapping its wings). A soaring bird is actually gliding downward but the air is rising more rapidly than the bird is sinking. A bird with a light wing loading can glide more slowly than a bird with a heavy wing loading and thus will rise more rapidly in a given updraft and and be able to use less powerful updrafts. Low wing loadings and lower stalling speeds also increase maneuverability.

Tails also contribute to lift, particularly in slow, soaring flight; this is why hawks spread their tails when soaring in an updraft. Although tails do not produce as much lift per unit area as wings, a bird with a longer tail and larger tail area when spread may have some advantage over a bird with a shorter tail and less tail area. This is because a folded tail induces little drag in flapping flight, need not be flapped as a wing, but is available for added lift when needed. The main advantage of increased tail area, however, is that it enhances maneuverability. Large "reserve" control area, as produced by a spread tail is of particular advantage at slow flight speeds since the force produced by a deflecting surface is proportional to the area of the surface and the square of air speed. Birds which fly rapidly thus need smaller control surfaces than those which fly slowly. (For a more detailed, yet comprehensible, explanation of bird flight see Barlee 1964.)

The above aerodynamic considerations lead to the conclusions presented below. The low wing loadings of juvenile sharp-shins give them the

potential of using lighter updrafts than adults, a capability which is further enhanced by the large tail area. Shorter wings require less power to flap and hence less energy consumption than longer-winged adults. All of these considerations suggest that juveniles expend less energy in flying than do adults. The light total surface loadings of juveniles provide them with inherently greater maneuverability than adults, with the large tail area playing an important role.

Adults weigh more than juveniles and this difference is almost certainly not the result of fat deposition and is most likely due to larger flight muscles in adults (Mueller et al. 1979). The greater weight, larger wing muscles, greater wing loading and greater aspect ratio of adults should produce a more rapid and powerful flight and a greater force in striking prey than that of juveniles, but at the expense of greater energy expenditure. The apparent loss in aerodynamic maneuverability in adults may well be compensated for by the greater power and experience of adults as compared to juveniles. Adults are thus faster, higher performance "flying machines" than juveniles, but require higher energy expenditures and thus higher food consumption than juveniles.

Adults thus appear to be an "optimal design" for rapid and powerful pursuit of prey and the juveniles a lower performance configuration, but one which is inherently more maneuverable and requires less energy consumption and expenditure. As juveniles gain experience they can afford the adult configuration; both aerodynamic forms are thus adaptive. Readers should be reminded that the above conclusions are based on morphometric measurements and aerodynamic considerations; direct measurements of performance and metabolic needs are lacking and would be extremely difficult, if not impossible, to obtain.

SUMMARY

Adult sharp-shins have significantly longer and wider wings, greater wing areas, higher wing loadings and higher aspect ratios than juveniles. Juveniles have longer tails and greater tail areas than adults. Within an age class, females are larger than males in all of the above measures except aspect ratio. The differences in aerodynamic characteristics between the age classes permit and obligate adults to fly faster, result in greater striking force at prey, and probably require more energy consumption than in juveniles. Juveniles are more maneuverable and probably require less energy in flight. The higher weight of adults is probably due to increased flight musculature and the added power, plus experience, probably compensate for the aerodynamic disadvantages of adults as compared to juveniles.

ACKNOWLEDGMENTS

Sandra Dziedzic and Patricia Christy traced and measured the photographs of the wings and tails and performed statistical calculations. N. S. Mueller and R. H. Wiley offered helpful comments on the manuscript. The fieldwork was aided by a grant from the Frank M. Chapman Memorial Fund.

LITERATURE CITED

BARLEE, J. 1964. Flight. Pp. 299–307 *in* A new dictionary of birds. (A. L. Thomson, ed.). Nelson, London, England.

BROWN, L. AND D. AMADON. 1968. Eagles, hawks, and falcons of the world. McGraw-Hill, New York, New York.

BUB, H. 1974. Vogelfang und Vogelberingung. Teil III. A. Ziemsen, Wittenberg-Lutherstadt, E. Germany.

MUELLER, H. C. AND D. D. BERGER. 1966. Analyses of weight and fat variations in transient Swainson's thrushes. Bird-Banding 37:83–112.

——— AND ———. 1967. Fall migration of Sharp-shinned Hawks. Wilson Bull. 79:397–415.

——— AND ———. 1970. Prey preferences in the Sharp-shinned Hawk: the role of sex, experience and motivation. Auk 87:452–457.

———, ——— AND G. ALLEZ. 1979. Age and sex differences in size of Sharp-shinned Hawks. Bird-Banding 50:34–44.

DEPT. ZOOLOGY AND CURRICULUM IN ECOLOGY, UNIV. NORTH CAROLINA, CHAPEL HILL, NORTH CAROLINA 27514 (HCM) AND CEDAR GROVE ORNITHOLOGICAL STATION, ROUTE 1, CEDAR GROVE, WISCONSIN 53013 (DDB, GA). ACCEPTED 19 MAR. 1981.

Wilson Bull., 93(4), 1981, pp. 500–505

EVIDENCE FOR AERODYNAMIC ADVANTAGES OF TAIL KEELING IN THE COMMON GRACKLE

Scott Hickman

The behavioral function of tail keeling in the Common Grackle (*Quiscalus quiscula*) has been thoroughly documented as a male flight display (Bent 1958; Ficken 1963; Wiens 1965; Maxwell 1970; Wiley 1976a, 1976b). The purpose of this study is to determine if keeling functions aerodynamically as well.

STUDY AREA AND METHODS

The data used in this study were collected through field observations of flying Common Grackles. A total of 3507 nonbreeding season observations was recorded from August 1974 through February 1975. Breeding season observations totaled 1415 and were recorded from March 1975 through May 1975. Observations were recorded in the vicinity of Bloomington–Normal, McLean Co., Belleville, St. Clair Co., and Carbondale, Perry Co., all in Illinois.

Each observation was a record of the configuration of the rectrices of a flying bird and its concomitant flight status. The tail configuration was recorded as one of four possible degrees of keeling: (1) flat tail—tail forms one plane (180°), (2) shallow keel—slight depression of midline rectrices folds the tail into a shallow V of approximately 160°, (3) medium keel—increased depression of central rectrices folds the tail into a deeper V of approximately 120°, (4) deep keel—complete depression of central rectrices in which the tail is folded into a deep V of less than approximately 110°. These 4 categories were selected because they represent the maximum number of keeling positions I could accurately distinguish. Observations which I could not clearly assign to any of these categories were disregarded.

In addition to a flying grackle's degree of keeling, I also recorded the following 14 characteristics: (1) sex—male or female; (2) season—breeding or nonbreeding; (3) relative wind direction—wind direction relative to bird flight direction; (4) wing speed—m/sec; (5) wind character—steady or gusty; (6) bird braking—yes or no; (7) bird banking—yes or no; (8) bird angle—ascending, descending or level flight; (9) company—bird accompanied or alone; (10) bird flight—flapping or gliding; (11) tail spread—tail fanned or not; (12) tail molting—yes or no; (13) entering roost—whether or not the bird was entering a roost; (14) leaving roost—whether or not the bird was leaving a roost.

I treated the 14 characteristics of bird status as independent variables and degree of tail keeling as the dependent variable. For mathematical analysis the 4 degrees of keeling (flat, shallow, medium and deep) were assigned the values 0, 1, 2 and 3, respectively. Stepwise multiple regression analysis was used to determine which independent variables, and/or combinations of independent variables, could account for a significant proportion of the variability in keel depth. Pearson product-moment correlations were also calculated. One-way analysis of variance was used to test for significant differences between mean degrees of tail keeling associated with each value of an independent variable. The breeding season and nonbreeding season data were treated separately, then pooled, for all statistical tests.

RESULTS

The results of the stepwise multiple regression analysis are shown in Tables 1, 2 and 3 for the nonbreeding season, breeding season and com-

TABLE 1
PARAMETERS ASSOCIATED WITH KEELING DURING THE NONBREEDING SEASON

Step and df	Independent variable	R^2	F	F[a]
1	Tail spread	0.368	1965	12.10
2	Company	0.426	1305	7.60
3	Banking	0.479	1077	5.91
4	Molting	0.487	845	5.00
5	Braking	0.494	648	4.52

[a] F value that must be exceeded to attain $P < 0.001$.

bined seasons data, respectively. These tables indicate the maximum cumulative percent variance accounted for (R^2) by independent variables. Table 4 indicates what mean keel depths are associated with various independent variable values.

Deep keel was displayed only during the breeding season and only by males. During the breeding season 50% of all observed males had their tails in deep keel. Deep keel was the only tail shape used more by one sex than the other.

Medium keel was rarely used by either sex. Only 4.5% of observed males and females showed medium keel.

Only nonbreeding season data are used to analyze shallow keel. This is because frequent sexual display of deep keel by males during the breeding season under virtually all conditions consistently increased the average keel depth correlated with each independent variable. This masked the actual relationship between aerodynamic factors and shallow keel.

Grackles that were braking, tail spreading, banking, ascending or with

TABLE 2
PARAMETERS ASSOCIATED WITH KEELING DURING THE BREEDING SEASON

Step and df	Independent variable	R^2	F	F[a]
1	Sex	0.228	416	12.10
2	Entering roost	0.302	305	7.60
3	Bird angle	0.320	221	5.91
4	Banking	0.331	174	5.00
5	Wind direction	0.341	145	4.52

[a] F value that must be exceeded to attain $P < 0.001$.

Table 3
Parameters Associated with Keeling for Combined Data

Step and df	Independent variable	R^2	F	F^a
1	Season	0.218	1373	12.10
2	Braking	0.273	926	7.60
3	Sex	0.315	757	5.91
4	Company	0.349	659	5.00
5	Banking	0.375	592	4.52
6	Entering roost	0.387	524	4.02
7	Leaving roost	0.394	479	3.72
8	Bird angle	0.409	427	3.48
9	Wind direction	0.413	385	3.30

[a] F value that must be exceeded to attain $P < 0.001$.

tails in molt often used shallow keel. Sixty-three percent of all braking, 64.9% of all tail spreading, 85% of all banking, 44.7% of all ascending and 42.2% of all tail molting birds used shallow keel. This shallow keel differed significantly ($P \leq 0.01$) from the nearly flat tail seen in the remaining contexts (Table 4). Flat tail was noted in only 24% of all braking, 23% of all tail spreading, 17% of all banking, 37% of all ascending and 22% of all tail molting grackles.

Eighty-six percent of all grackles flying into a head wind used flat tail. This represents at least 11% more use than flat tail generated with any other wind direction. Flat tail was also the configuration most used for level, non-maneuvering flight such as when flying to or from a roost. Approximately 90% of all grackles entering or leaving a roost possessed flat tail and 88% of all grackles recorded as flying level and not banking had their tails in a flat position.

DISCUSSION

Aerodynamic factors account for variability in keel depth. Table 1 shows that tail spread (usually associated with landing), banking, tail molting and braking are significant predictors of keel depth during the nonbreeding season. Similarly, Table 2 indicates that bird angle, banking and wind direction account for variance in keel depth during the breeding season and braking, banking, bird angle and wind direction are predictors of keel depth when the seasonal data are pooled. This is evidence that tail keeling has aerodynamic functions.

The most likely aerodynamic uses of tail keeling are stall prevention and improvement of stability. Grackles observed to be landing, banking, taking off, or with tails in molt typically possessed shallow keel. These are

TABLE 4
KEEL DEPTHS ASSOCIATED WITH VARIOUS INDEPENDENT VARIABLES (NONBREEDING SEASON)

Independent variables	$\bar{x}$	SE	N
Braking			
No	0.12*	0.0070	2953
Yes	0.90*	0.0250	555
Tail spread			
No	0.11*	0.0065	2905
Yes	0.90*	0.0239	601
Bird angle			
Level	0.40*	0.0337	66
Descending	0.30*	0.0091	3125
Ascending	0.80*	0.0235	317
Banking			
No	0.20*	0.0079	3202
Yes	1.0*	0.2150	305
Molting			
No	0.41*	0.0075	3072
Yes	0.80*	0.0344	436

* Significant at $P < 0.001$.

all conditions during which birds are susceptible to stall and/or are unstable.

Landing birds are flying slowly and in danger of stalling since lift is directly proportional to air speed. Birds typically prevent stalls during landing by spreading and depressing the flat tail which draws the airflow down and caudally from the dorsal surfaces of the wings. This keeps the airflow from breaking away from the wing surfaces and prevents stalling (Pennycuick 1972). Landing grackles, however, did not usually possess a flat tail. Grackles that were landing were most often recorded as tail spread and braking. The correlations in the results section and Table 4 indicate that these grackles used shallow keel rather than the flat tail described above. Shallow keel may be more effective in stall prevention than flat tail since depression of the central rectrices may funnel air downward from the wings more effectively.

Shallow keel may also reduce the instability encountered during landing. When used as an air brake the flat tail would create some directional instability to be controlled by the wings. However, shallow keel positions the ventral surface of the braking tail into a wedge, thereby giving the spread tail a guiding quality which increases landing precision. The dorsal surface of a tail in shallow keel could also aid in the development of

increased landing precision as it may funnel the caudal airflow into a longitudinal axis and thereby minimize yaw.

Grackles normally used shallow keel while banking (Table 4). This may also be functionally interpreted in terms of stall prevention and increased flight stability. Birds are susceptible to stall during banking (Dalton 1977). Positioning the tail in shallow keel while banking may function to prevent stalls as described above. Stability is also reduced during banking because the bird's body passes through a vertical rather than horizontal plane. Airfoils are not parallel to the ground and are less efficient in resisting gravity and regulating yaw. Shallow keel, however, would increase the stability of a turn by making the tail a 2-plane surface that would funnel the airflow into a longitudinal axis and minimize yaw.

The mean keel depth used in ascending flight also approximated shallow keel (Table 4). Most ascending grackles were observed while taking flight. During take-off, air speed is slow and thus conducive to stall (Salt 1966). Shallow keel may prevent stalling during take-off in the same manner as proposed above for landing and banking.

Most grackles used shallow keel while their tails were in molt, this shallow keel being significantly deeper than that of grackles with tails not in molt (Table 4). Many birds with tails in molt had no full length rectrices. Such an abnormally short tail cannot provide the stability of a full length tail. Shallow keel would presumably help to regain the stability lost during tail molt.

Shallow keel seems to be the only recorded keel shape that is primarily aerodynamic in function. Deep keel was correlated with behavioral rather than aerodynamic conditions. This caused sex to account for more of the variability in the breeding season data than did any other independent variable (Table 2). This is in agreement with the conclusions of earlier researchers that keeling functions behaviorally. Medium keel was seldom used by Common Grackles of either sex. It seems to exist only as an intermediate position through which the tail passes when changing from shallow keel to deep keel or vice versa. Flat tail functions in several displays performed by this species (Ficken 1963; Wiley 1976a, 1976b). My results indicate that the aerodynamic situations during which grackles most often use flat tail are (1) when flying into a head wind, apparently because keels increase drag inordinately during head winds; and (2) in level and non-maneuvering flight, as when grackles fly to or from a roost. During these conditions the tail's aerodynamic importance is relatively minimal. The wings can supply all the lift, thrust and control required to maintain trim. The tail is then most efficiently positioned in a flat, narrow shape to minimize drag.

The aerodynamic uses proposed above for shallow keel are hypothetical

functions based upon the correlations between shallow keel and conditions during which birds are unstable and/or susceptible to stall. These hypotheses are strengthened by unquantified observations which indicate that other birds, such as the Rock Dove (*Columba livia*) and Herring Gull (*Larus argentatus*) also use shallow (but U vs V shaped) keel under unstable conditions during which stall is likely.

I am publishing my conclusions even though I am uncomfortable with the degree to which they rely on pure correlations in the hope that researchers with wind tunnel access will properly test the aerodynamic functions proposed for shallow keel.

SUMMARY

This study indicates that tail keeling by Common Grackles functions aerodynamically as well as behaviorally. Deep keel functions behaviorally and is restricted to males. Medium keel was rarely observed. The primary function of shallow keel is probably aerodynamic, increasing stability during tail molt. Shallow keel probably also functions to prevent stalls during landing, banking and take-off. The Common Grackle showed flat tail in direct non-maneuvering flight and when flying into head winds.

ACKNOWLEDGMENTS

I would like to thank the members of my thesis committee, Dale Birkenholz, Larry Cadwell and Jared Verner for their aid throughout this study. I also thank Dale Birkenholz, Thomas Poulson and John Mathwig for reviewing an earlier draft of this paper.

LITERATURE CITED

Bent, A. C. 1958. Life histories of North American blackbirds, orioles, tanagers, and allies. U.S. Natl. Mus. Bull. 211.

Dalton, S. 1977. The miracle of flight. McGraw-Hill Book Co., New York, New York.

Ficken, R. W. 1963. Courtship and agonistic behavior of the Common Grackle, *Quiscalus quiscula*. Auk 80:52–72.

Maxwell, G. R. 1970. Pair formation, nest building, and egg laying of the Common Grackle in northern Ohio. Ohio J. Sci. 70:284–291.

Pennycuick, C. J. 1972. Animal flight. Edward Arnold Publ., London, England.

Salt, W. R. 1966. An adaptation to produce large lift forces in small short-winged birds. Can. J. Zool. 44:1037–1040.

Wiens, J. A. 1965. Behavioral interactions of Red-winged Blackbirds and Common Grackles on a common breeding ground. Auk 82:356–374.

Wiley, R. H. 1976a. Affiliation between the sexes in Common Grackles I: specificity and seasonal progression. Z. Tierpsychol. 40:59–79.

———. 1976b. Communication and spatial relationships in a colony of Common Grackles. Anim. Behav. 24:570–584.

DEPT. BIOLOGY, ILLINOIS STATE UNIV., NORMAL, ILLINOIS 61761. (PRESENT ADDRESS: DEPT. BIOLOGY, COLL. LAKE COUNTY, GRAYSLAKE, ILLINOIS 60030 AND DEPT. BIOLOGY, UNIV. ILLINOIS AT CHICAGO CIRCLE, CHICAGO, ILLINOIS 60080.) ACCEPTED 5 MAR. 1981.

Wilson Bull., 93(4), 1981, pp. 506–518

REPRODUCTIVE CORRELATES OF ENVIRONMENTAL VARIATION AND NICHE EXPANSION IN THE CAVE SWALLOW IN TEXAS

Robert F. Martin

Natural and anthropogenic environmental factors interact to form the selective background that shapes the reproductive variability of many avian species. An excellent subject for investigations of such interactions is the Cave Swallow (*Petrochelidon fulva*), a relatively widespread cavern-nesting species presently undergoing human-mediated breakdown of ecological segregation from other swallows at the northeastern periphery of its range in North America. Martin (1974, 1980), Martin and Selander (1975), and Martin and Martin (1978) have discussed range expansion and intergeneric hybridization as consequences of highway culvert nesting in this species, while Martin et al. (1977) outlined the basic pattern of reproduction of a cavern-nesting colony. At the cavern site, minimal or nonexistent nest predation and interspecific competition, little human disturbance, constant availability of nesting material and minimal temperature fluctuation operate together to increase environmental stability, and enhance the value of correlations between patterns of reproduction and the few environmental factors that do fluctuate here. Such diminished ecological variability resembles that characteristic of islands (MacArthur and Wilson 1967; Cody 1966, 1971) and suggests comparisons of the reproductive parameters of cavern populations of *P. fulva* with those of culvert colonies exposed to more variable selective influences. In this report, I (1) document variation in reproduction in an isolated cave colony of *P. fulva* in successive years; (2) use these data to test the general hypothesis that directly relates reproductive output and success to amount of precipitation in xeric areas; and (3) contrast reproductive patterns of cave and culvert populations of this species and discuss possible reasons for their disparity.

STUDY AREA AND METHODS

During 1974 and 1975, data were taken at an isolated colony of Cave Swallows nesting at Dunbar Cave, 37 km WSW Rocksprings, Edwards Co., Texas. Additionally in 1974, Cave Swallow colonies that nested syntopically with Barn Swallows (*Hirundo rustica*) in four highway culverts were visited; these were located in Kinney and Uvalde counties, approximately 73 km SE of the cave site, along 23 km of U.S. Highway 90 beginning at and extending eastward from 13 km E of Brackettville. All sites lie just east of the Chihuahuan Desert in a region of gently rolling, sparsely vegetated hills dissected by semi-permanent and temporary streams.

Table 1

Study Area Precipitation (1974 and 1975) in cm Preceding and During First and Second Reproductive Cycles of Cave Swallows[1]

	Precipitation			
	1974 (Dry)		1975 (Wet)	
Location	Jan.–May[2]	Jan.–July[3]	Jan.–May	Jan.–July
Carta Valley (13 km W cave)	13.20	16.70	22.89	44.39
Rocksprings (40 km NW cave)	17.45	20.40	36.58	55.65
Brackettville (59 km SSE cave)	15.11	16.64	29.85	51.79

[1] Data from NOAA 1974, 1975, 1976.
[2] Period precedes and includes first reproductive cycle of season.
[3] Period precedes and includes first and second reproductive cycles.

Precipitation and temperature data (NOAA 1973, 1974, 1975) from Carta Valley (29°48′N, 100°48′W), 13 km W of Dunbar Cave, and from Brackettville (29°19′N, 100°24′W) were considered representative of those at cave and culvert sites, respectively; Table 1 presents rainfall data for these and for other reference sites in the cave area. Ambient temperatures at representative nest-sites were monitored with recording thermographs.

Dunbar Cave opens by a vertical shaft approximately 2.3 m in diameter and 3.4 m in length into the roof of a chamber nearly 25 m in greatest diameter and 5 m in height. Here, a colony of from 250–300 pairs of *P. fulva* nested in isolation from other birds. Nests were flared-rim cups, fashioned of mud or guano pellets, and usually attached high on walls or in pockets eroded in the cave ceiling.

Sample culverts were of multiple-passageway concrete construction and were selected from a series of 16 culverts that averaged 1.6 km apart. The series averaged ca. 17 breeding pairs of swallows (*P. fulva* and *H. rustica*) per culvert; culverts with greater concentrations of swallows usually were separated by culverts possessing considerably fewer birds; no culvert held over 80 breeding pairs. The four sample culverts held from 6–32 nesting pairs of *P. fulva*; *H. rustica* formed 49% of the overall total of breeding swallows in these culverts. Culverts 54, 51, 48 and 40 had 6, 5, 11 and 10 passages, respectively, that averaged 15.1 m × 1.6 m × 1.7 m (length × width × height). Nests of both *P. fulva* and *H. rustica* usually were built on culvert walls within 0.3 m of their ceilings.

Nests were identified individually by inserting numbered nails into nest bases or by marking adjacent surfaces with pencil. Active nests accessible by ladder formed the annual samples at Dunbar Cave; approximately 40% of the nests of the colony were marked. During 1974, nest contents usually were examined at 2- to 3-day intervals; a total of 35 visits was made to the cave (Fig. 1). Fifty-two visits were made to the site in 1975. Early in the 1975 season, during three periods of 6, 10 and 9 days (Fig. 1), nest contents were examined daily to determine incubation and nestling periods; before and between these periods of daily visitation and after 8 June 1975, the 1975 visitation schedule approximated that of 1974. Culverts were visited in 1974 on the same days as cave visits.

Since *P. fulva* lay on successive days until clutch completion, clutch initiation dates not

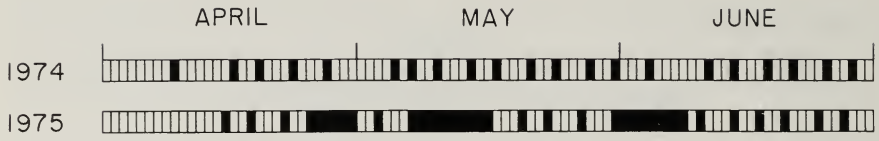


FIG. 1. Investigator nest-visitation schedules at Dunbar Cave during the first reproductive cycle of 1974 and of 1975. Small black rectangles represent dates on which nests were visited by the investigator; small vacant rectangles, dates on which nests were not visited.

known precisely were determined by backdating from the sampling day on which eggs first were found in the nest; similarly, clutch completion dates were determined by forward dating to account for all eggs observed. When hatch time was not known exactly, the average incubation period of 15 days (Martin et al. 1977) was substituted. Due to our sampling schedule, "hatch" data may include very early nestling mortality (Martin et al. 1977). Egg loss and nestling mortality to 19 days post-hatch (1 day prior to flight potential) arbitrarily were assigned to the midpoints of the sampling gaps during which they occurred.

Due to the more intensive (daily) visitation program in early 1975, more precise hatch and survival data were available for nests examined during this period than for those visited at other times. These daily data were not used in scoring of reproductive events reported here; for this purpose, only data gathered on visits of a predetermined schedule that approximated the regular (2–3-day interval) schedule were used (Fig. 1). Except for comparisons of correlation coefficients, or where noted otherwise, statistical comparisons employed the Mann-Whitney *U*-test (Sokal and Rohlf 1969). Results of statistical tests were considered significant at $P < 0.05$.

RESULTS

Environmental variables.—Precipitation data for periods preceding and during the 1974 and 1975 reproductive seasons of the cave population and the 1974 reproductive season of the culvert populations are presented in Table 1. Precipitation in the area of Dunbar Cave was considerably greater in 1975 than in 1974. Precipitation at the culvert area was only slightly higher than at Dunbar Cave in 1974. Breeding season (April–August) mean temperatures at the area surrounding Dunbar Cave were similar in 1974 (25.6°C) and 1975 (24.3°C). Temperature records for the culvert area are incomplete for June 1974, but the cumulative mean for the remaining months of the breeding season approximates that for the cave area (cave–25.1°C; culverts–24.4°C) in 1974. The thermal regime at cave nests during the breeding season (17–22°C, season minima and maxima; 3°C maximum daily fluctuation) was less variable than that at a sample culvert (14–32°C, season minima and maxima; 8°C maximum daily fluctuation). A moist substrate of mud and guano provided a constantly available source of nesting material to the cave colony, while culvert-nesting birds frequently travelled longer distances to gather mud. The potential of catastrophic loss due to flooding existed for culvert, but not cave populations.

The cave population also was exposed to fewer biotic variables. No other swallows nested near Dunbar Cave, while culvert *P. fulva* nested syntopically with nearly equal numbers (49%, 1974) of Barn Swallows. Vertebrate nest predators were not seen at Dunbar Cave, nor is it likely that they could pose a serious threat at such a site. Eggs and nestlings in culverts were exposed to attack or predation by at least six species of mammals, two species of birds and six species of snakes, in addition to ants and several other invertebrates (Martin, unpubl.). Casual human disturbance is minimal at Dunbar Cave because the cavern is non-commercial, lies on private property and entry is difficult without specialized equipment. Culvert colonies, however, are disturbed regularly by itinerants and highway maintenance crews. Although catastrophic losses due to deliberate human perturbation occur occasionally in culverts, none occurred in sample culverts in 1974.

Reproduction at Dunbar Cave.—Clutch-size ranged from 1–6 eggs. Clutches of 3–5 eggs comprised 96.3% of all clutches (Tables 2, 3) and clutches of one, two and six eggs comrpised, respectively, 0.9%, 2.6% and 0.2% of all clutches. Clutches were divided arbitrarily into early and late categories according to waves of synchrony in laying. Comparative distributive statistics for clutch-size, hatch (no. of young hatched) and survival (no. of young surviving to 19 days) of these and total first and later clutches of 1974 and 1975 are presented in Table 2. Overall percentage values of hatched young/eggs laid, surviving nestlings/hatched young, and surviving nestlings/eggs laid, also are presented in Table 2. Table 4 depicts a matrix of results of statistical testing relating fecundity and reproductive success to precipitation in the study area.

Clutch-size, hatch and survival decreased with time within and between clutch categories in 1974 (Tables 2, 4); these decreases were statistically significant (Table 4). In 1975, clutch-size decreased significantly within and between clutch categories (Table 4). Although hatch and survival in 1975 decreased between early and late first clutches, these decreases were not statistically significant (Table 4). Hatch and survival decreased significantly between early and late second clutches in 1975 (Table 4). No significant differences in hatch and survival occurred between first and second clutches in 1975.

To assess the effects of differential perturbation, comparisons of data for 56 nests in which contents (eggs and nestlings) were marked and 70 in which contents were unmarked were made for first clutches of 1975. Hatch was not significantly lower in nests with marked eggs (2.71 ± 0.20, marked vs 3.00 ± 0.16, unmarked; $0.1 > P > 0.05$, NS). Survival was significantly lower in nests with marked contents (2.43 ± 0.18, marked vs 2.84 ± 0.15, unmarked; $P < 0.05$). Comparisons of hatch percentage and survival/hatch percentage indicated that the former was 17% lower in nests with

Table 2

Reproductive Statistics and Hatch-survival Percentages for Nests of *P. fulva* at Dunbar Cave (1974 and 1975) and Culvert Sites (1974)

Clutch sequence[1]	N	Clutch-size $\bar{x} \pm SE$	Young hatched $\bar{x} \pm SE$	Survival (19 days) $\bar{x} \pm SE$	Hatch/ laid	Survive/ hatch	Survive/ laid
Cave 1974							
Clutch 1 early (before 11 May)	87	3.95 ± 0.069	3.26 ± 0.133	2.78 ± 0.145	0.82	0.85	0.70
Clutch 1 late (11 May–1 July)	28	3.61 ± 0.129	2.86 ± 0.250	1.75 ± 0.227	0.79	0.61	0.49
Clutch 2 early (before 30 June)	65	3.45 ± 0.102	2.55 ± 0.140	1.31 ± 0.141	0.74	0.51	0.38
Clutch 2 late (July)	8	2.75 ± 0.163	1.00 ± 0.499	0.63 ± 0.419	0.36	0.63	0.23
Total clutch 1	115	3.87 ± 0.062	3.17 ± 0.118	2.53 ± 0.129	0.81	0.80	0.65
Total clutch 2	73	3.37 ± 0.096	2.40 ± 0.146	1.22 ± 0.136	0.71	0.52	0.37
Total (1 + 2)	188				0.78	0.71	0.54
Cave 1975							
Clutch 1 early (before 11 May)	111	4.03 ± 0.057	2.93 ± 0.128	2.67 ± 0.125	0.73	0.91	0.66
Clutch 1 late (11 May–1 July)	15	3.47 ± 0.133	2.47 ± 0.412	2.33 ± 0.398	0.71	0.95	0.67
Clutch 2 early (before 30 June)	99	3.71 ± 0.052	3.18 ± 0.105	2.81 ± 0.125	0.86	0.88	0.76
Clutch 2 late (July)	8	2.88 ± 0.294	2.38 ± 0.323	2.13 ± 0.295	0.83	0.89	0.74
Total clutch 1	126	3.96 ± 0.055	2.87 ± 0.123	2.63 ± 0.120	0.73	0.91	0.66
Total clutch 2	107	3.64 ± 0.056	3.12 ± 0.102	2.76 ± 0.119	0.86	0.88	0.76
Total clutch 3	8	3.13 ± 0.124	2.00 ± 0.597	2.00 ± 0.597	0.64	1.00	0.64
Total (1 + 2 + 3)	241				0.78	0.90	0.70
Culverts 1974							
Total clutch 1	81	4.31 ± 0.065	3.44 ± 0.119	3.25 ± 0.127	0.79	0.94	0.75
Total clutch 2	49	3.96 ± 0.087	3.22 ± 0.166	2.92 ± 0.184	0.81	0.90	0.74
Total clutch 3	8	3.50 ± 0.188	2.38 ± 0.564	1.63 ± 0.497	0.68	0.16	0.11
Total (1 + 2 + 3)	138				0.79	0.90	0.72

[1] Chronology by nest, not adult pair; adults unmarked.

TABLE 3

NESTLING SURVIVAL (TO 19 DAYS) IN RELATION TO MOST COMMON CLUTCH-SIZES IN *P. FULVA*

	Clutch-size	Frequency	% nestlings surviving	Nestling survival per brood ($\bar{x}$)
Cave (1974)				
Clutch 1	3	22	70	2.10
	4	76	65	2.60
	5	14	63	3.15
Clutch 2	3	34	42	1.26
	4	31	35	1.39
Cave (1975)				
Clutch 1	3	24	74	2.22
	4	80	65	2.60
	5	21	66	3.30
Clutch 2	3	29	76	2.28
	4	72	76	3.05
Culvert (1974)				
Clutch 1	3	5	87	2.61
	4	46	84	3.36
	5	30	64	3.20
Clutch 2	3	10	67	2.00
	4	31	75	3.00

marked contents (63% vs 80%), while the latter was only 1% lower (91% vs 92%).

No significant differences in clutch-size, hatch and survival existed between 1974 and 1975 first clutches (early, late and total). However, second-clutch size, hatch and survival increased from 1974–1975; with one exception (size of late second clutch), these differences were statistically significant (Table 4).

When cumulative reproductive data for both clutches of 1974 and 1975 were compared (Table 2; total 1 + 2 vs total 1 + 2 + 3), hatch percentages were equal, but nestling survival percentages were considerably higher in 1975. These differences were due primarily to very high nestling survival within the second brood of 1975 (Table 2).

Mean nestling survival per brood increased with clutch-size in both clutches of both study years at Dunbar Cave (Table 3); three of four correlation coefficients calculated for Dunbar Cave clutches indicated a moderate, but significant positive correlation between them (Table 5).

Table 4

Statistical Comparisons among Samples Represented by Clutch-size, Hatch and Survival Means for 1974 and 1975 *P. fulva* Clutches at Dunbar Cave[1]

	Clutch-size			Hatch			Survive		
	1974 Dry		1975 Wet	1974 Dry		1975 Wet	1974 Dry		1975 Wet
Clutch 1									
Early	3.95	NS	4.03+	3.26	NS	2.93+	2.78	NS	2.67+
	*		***	*		NS	***		NS
Late	3.61	NS	3.47+	2.86	NS	2.47+	1.75	NS	2.33+
Clutch 2									
Early	3.45	**	3.71	2.55	***	3.18	1.31	***	2.81
	**		**	**		**	*		*
Late	2.75	NS	2.88	1.00	*	2.38	0.63	*	2.13
Total clutches									
1	3.87	NS	3.96+	3.17	NS	2.87+	2.53	NS	2.63+
	***		***	***		NS	***		NS
2	3.37	**	3.64	2.40	***	3.12	1.22	***	2.76
			**			*			NS
3			3.13			2.00			2.00

[1] Asterisks appear (vertically and horizontally) between means representing samples between which statistically significant 1-tailed Mann-Whitney *U*-tests were performed (* $P < 0.05$; ** $P < 0.01$; *** $P < 0.001$. NS = results not significant. Hypothesis tested: fecundity and reproductive success are directly related to amount of precipitation in xeric areas.
+ follows data for nests periodically under daily observation.

The number of nests in the sample area increased approximately 10% from 1974–1975 (Tables 2, 6). Sixty-three percent of nests that held an early clutch in 1974 received a second clutch, while 84% of the 1975 nests were laid in a second time (Tables 2, 6). Largely due to increased second-clutch size and nestling survival, 261 more young survived to 19 days in

Table 5

Relationships (regression equations and correlation coefficients) between Nestling Survival (Y) and Clutch-size (X)

		Clutch 1		Clutch 2	
Location	Year	Regression equation	*r*	Regression equation	*r*
Cave	1974	$Y = -0.043 + 0.663X$	0.318**[1]	$Y = 0.329 + 0.272X$	0.192
Cave	1975	$Y = 0.263 + 0.597X$	0.276**	$Y = -0.514 + 0.898X$	0.426***
Culvert	1974	$Y = 2.950 + 0.067X$	0.034	$Y = -0.359 + 0.828X$	0.392**

[1] Asterisks follow correlation coefficients that are statistically significant (** $P < 0.01$; *** $P < 0.001$).

TABLE 6
NUMBERS OF NESTLINGS SURVIVING TO 19 DAYS AT CAVE AND CULVERT STUDY SITES

	Dunbar Cave				Culvert sites	
	1974		1975		1974	
	# Young	# Nests	# Young	# Nests	# Young	# Nests
Clutch 1	290	115	331	126	263	81
Clutch 2	91	73	295	107	143	49
Clutch 3	—	—	16	8	13	8
Total	381		642		419	

the sampled area in 1975 than in 1974, an increase in survival of 40% (Table 6).

Reproduction at culvert sites.—Clutch-size for 1974 culvert-nesting *P. fulva* ranged from 3–5 (Table 3). Distributive statistics for grouped culvert-site reproductive data are shown in Table 2. Since separate culverts were involved, overall nesting synchrony was reduced (see, also, Myres 1957) and chronological (early–late) dichotomies could not be assigned within clutches. As in cave-nesting *P. fulva*, clutch-size, hatch and survival decreased in culvert birds from first to second clutches (Table 2); of these decreases, only that between clutch-size of clutches one and two was statistically significant ($P < 0.005$). Reproductive parameters declined further in the few third clutches deposited. Hatch and survival percentages of first and second clutches were similar (Table 2).

Mean nestling survival per brood increased from clutches of three to clutches of four for the first clutch, but decreased slightly for clutches of five (Table 3); the correlation coefficient for these variates was not significant (Table 5). Mean nestling survival per brood increased with clutch-size in the second clutch (Table 3); the correlation coefficient for these variates was statistically significant (Table 5).

Comparisons between cave and culvert populations.—Clutch-size, hatch and nestling survival of first and second clutches were higher for the culvert populations than for the cave colony in 1974 (Table 2); with one exception (first clutch hatch $0.1 > P > 0.05$, NS), these differences were highly significant ($P < 0.001$). In 1974, a third clutch was deposited in some culvert nests, but in no cave nests (Table 2). Overall (total) hatch percentages were similar at culvert and cave in 1974, but total survival

percentages were considerably higher at culvert colonies (Table 2). At the culvert sites, approximately 30% fewer nests produced a total of about 10% more surviving nestlings (Tables 2, 6); much of this difference was due to high second clutch reproductive success.

DISCUSSION

Pattern of food availability generally is considered a major determinant of variation in avian reproduction (Lack 1954; Klomp 1970; Cody 1971; Ricklefs 1969, 1973; von Haartman 1971; Dingle and Khamala 1972; Immelmann 1973; Bryant 1975). Other environmental factors, in turn, influence food availability and also may affect reproduction in other ways. Much information relating reproductive parameters of birds to precipitation has developed in the past few decades; in arid regions, reproductive timing and success appear particularly closely tied to the pattern of rainfall (for example, Moreau 1944; Lack 1954; Keast and Marshall 1954; Immelmann 1963, 1973; Dingle and Khamala 1972; Sinclair 1978). Amount of rainfall frequently appears to influence reproduction through food chain effects but also may affect reproduction indirectly if the availability of nesting material and nest concealment are altered. Although Cave Swallows are constrained in nest building by scarcity of mud in some areas (Baker 1962), neither this moisture-dependent limitation, nor that of nest concealment by foliage are operative at Dunbar Cave (although the former may be a factor at culvert sites), and it is assumed that moisture-related constraints, if operative here, influence reproduction primarily through limitation of food resources.

Seasonal variation in reproductive parameters.—The seasonal decrease in clutch-size exhibited by *P. fulva* is typical of some populations of Cliff Swallow (*P. phrrhonota*) and *H. rustica*, swallows with which it nests syntopically (Samuel 1971, Graber et al. 1972, Anthony and Ely 1976, Grant and Quay 1977), as well as other passerines (Lack 1954, Klomp 1970, von Haartman 1971, other reviews). In *P. fulva*, hatch and nestling survival usually decline seasonally also (Tables 2, 4; Martin, unpubl.); these declines are particularly evident when the perturbed first clutch of 1975 is excluded from comparisons. The effect of day length on foraging time and that of prevailing regional precipitation pattern on food resources may determine seasonal (between-clutch) differences in avian fecundity (Lack 1954, Klomp 1970). Day length does not appear to be an important factor at the present study areas, however, for maximum day length occurs here just past the midpoint of the period including the first and second reproductive cycles. A stronger argument may be made for precipitation as an indirect determinant of seasonal productivity of *P. fulva*. In this region, a bimodal annual pattern of rainfall exists, with maxima occurring during April, May

TABLE 7

SEASONAL PRECIPITATION AND TEMPERATURE PATTERNS FOR REGION INCLUDING STUDY AREAS (35 YEAR AVERAGES)

Month	Mean monthly precipitation (cm)	Mean monthly maximum temperature (°C)
Jan.	2.36	16.4
Feb.	2.92	18.9
Mar.	2.29	22.9
Apr.	5.88	28.3
May	7.37	30.8
June	7.54	33.2
July	3.84	36.2
Aug.	4.72	35.9
Sept.	7.59	32.6
Oct.	5.33	27.3
Nov.	2.06	21.9
Dec.	2.29	17.7

and June, and again in September and October (Table 7; NOAA 1975, 1976). During the breeding season, precipitation usually is lowest during July and early August, during the second reproductive cycle. In addition, temperature is maximal during this period (NOAA 1974, 1976), and contributes to moisture deficiency through evaporation.

Annual variation in reproductive parameters.—At Dunbar Cave, a greater number of second clutches, in concert with increased clutch-size, hatch and survival within second clutches, contributed to make the wet reproductive season of 1975 considerably more productive than the relatively dry season of 1974 (Tables 1, 2, 4, 6). Similar patterns of high fecundity during years of high rainfall and abundant food resources (Hoesch 1936, Guirtchitch 1937, Moreau 1944, Lack 1954) or of dependence of reproduction on precipitation (Keast and Marshall 1954, Immelmann 1963, Collias and Collias 1978, Sinclair 1978) have been well documented in arid regions.

First clutch reproductive parameters of the Dunbar Cave colony did not increase markedly from 1974–1975. This was not unexpected, considering the increased perturbation to which individual nests and the entire colony were subjected during the first reproductive cycle of 1975 (Methods, also Fig. 1). Data taken under perturbed conditions may be of somewhat limited value for comparative purposes, but the environment of much of the North Temperate Zone is heavily disturbed (Lack 1965), and data reflecting quan-

titatively the potential effects of methodology are relevant. The lower survival in nests whose contents were marked appeared to be due largely to low hatchability. Losses ascribed to desertion occurred at approximately equal frequency in both marked (10%) and unmarked (11%) samples. These intra-clutch data represent only the proximal individual effects of marking and must be considered together with the more widespread and concomitant effects expected from disturbance of the entire colony: potential impairment of synchrony and attentiveness, and disruption of nestling and adult feeding patterns.

Comparisons between cave and culvert populations (1974).—Disturbance by humans is not a normal phenomenon at Dunbar Cave, but colonies of *P. fulva* that nest in highway culverts have undergone regular anthropogenic disturbance and risk and are subjected to other catastrophic and non-catastrophic biological and physical influences to which the cave colony is not exposed. Populations evolving in variable environments often display greater reproductive effort than those adapted to more stable conditions; theoretically, this increased effort balances increased mortality (Cody 1966, 1971). First and second clutches were larger in culvert populations than at Dunbar Cave and third clutches occurred only at culvert sites in 1974. Hatch and nestling survival of first and second clutches were higher in culverts as were overall hatching and survival percentages, the greatest difference appearing in comparisons between second clutches. Following Cody's postulations (1966, 1971), an ultimate interpretation of the data would be that differential mortality between culvert and cave populations (culvert mortality > cave) must occur at or after fledging. I believe that this is probable; recently fledged *P. fulva* usually remain in the vicinity of the culvert and return to the nest for several days, and, lacking in-flight strength and maneuverability, are exposed heavily to the hazard of vehicle strike. Relevant to the evaluation of this interpretation are the estimated maximal chronological separation of culvert from cave populations (20 generations) and the distance between them (65–80 km).

Density-dependent effects may be involved in the higher fecundity, hatch and nestling survival of culvert-nesting *P. fulva*; in other species such relationships are well documented for clutch-size, less adequately so for nestling survival (Klomp 1970, von Haartman 1971). Culvert nesting has been established only recently in central Texas, and has resulted in marked range expansion (Martin and Martin 1978). Although the culverts sampled in this study are not at the current edge of the range of *P. fulva*, their swallow densities (both conspecific and cumulative) are lower than at Dunbar Cave.

SUMMARY

Data on reproduction from Texas cave and culvert sites are presented for the Cave Swallow (*Petrochelidon fulva*), a peripheral U.S. species presently undergoing breakdown in ecological segregation at the northern margin of its range through modification of its nesting habits. Correlations exist between environmental influences, both natural and anthropogenic, and variation in pattern of reproduction of cave- and culvert-nesting colonies of this species. Seasonal declines in reproductive parameters occurred at both sites and are considered to reflect adaptations to within-season increasing aridity and diminished food supply. During a relatively wet year at a cavern-nesting colony, overall seasonal reproductive output and nestling survival were higher than during a drier year; much of this difference was due to significantly increased second clutch reproductive parameters. Increased investigator visitation of the cave colony during the first reproductive cycle of the wet year may have negatively affected hatch and survival of that year's first clutch. Culvert-nesting populations displayed significantly higher clutch-size and nestling survival than did the population nesting at the more typical cave site.

ACKNOWLEDGMENTS

Sallie Martin initiated the culvert research, provided much encouragement and support and improved the manuscript. W. F. Blair and Robert K. Selander offered useful suggestions. M. R. Lewis gathered most of the data. The Texas Highway Department permitted marking within culverts. Walter R. Davis, III, assisted in selection of the cave site and Mr. and Mrs. Robert Erekson graciously provided site access. Mark and Sallie Martin assisted during an exploratory visit to Dunbar Cave. R. F. Johnston, C. R. Brown and Jon C. Barlow reviewed and improved the manuscript. Portions of the research were supported by the National Geographic Society (Grant Nos. 1301, 1418 and 1721) and The Texas Memorial Museum.

LITERATURE CITED

Anthony, L. W. and C. A. Ely. 1976. Breeding biology of Barn Swallows in west-central Kansas. Bull. Kansas Ornithol. Soc. 27:37–43.

Baker, J. K. 1962. Associations of Cave Swallows with Cliff and Barn swallows. Condor 64:326.

Bryant, D. M. 1975. Breeding biology of House Martins *Delichon urbica* in relation to aerial insect abundance. Ibis 117:180–216.

Cody, M. L. 1966. A general theory of clutch-size. Evolution 20:174–184.

———. 1971. Ecological aspects of reproduction. Pp. 461–517 *in* Avian biology, Vol. 1 (D. S. Farner and J. R. King, eds.). Academic Press, New York, New York.

Collias, N. E. and E. C. Collias. 1978. Cooperative breeding behavior in the White-browed Sparrow Weaver. Auk 95:472–484.

Dingle, H. and C. P. M. Khamala. 1972. Seasonal changes in insect abundance and biomass in an East African grassland with reference to breeding and migration in birds. Ardea 59:216–221.

Graber, R. R., J. W. Graber and E. L. Kirk. 1972. Illinois birds: Hirundinidae. Illinois Nat. Hist. Surv. Biol. Notes 80:1–36.

Grant, G. S. and T. L. Quay. 1977. Breeding biology of Cliff Swallows in Virginia. Wilson Bull. 89:286–290.

Guirtchitch, G. 1937. Chronique ornithologie tunisienne pour l'annee 1936. Oiseau 7:450–472.

Hoesch, W. 1936. Nester und Gelege aus dem Damaraland. II. J. Orn. 84:3–20.

Immelmann, K. 1963. Drought adaptations in desert birds. Pp. 649–657 *in* Proc. 13th Int. Ornithol. Congr.

———. 1973. Role of the environment in reproduction as source of "predictive" information. Pp. 121–147 *in* Breeding biology of birds (D. S. Farner, ed.). Natl. Acad. Sci., Washington, D.C.

Keast, J. A. and A. J. Marshall. 1954. The influence of drought and rainfall on reproduction in Australian desert birds. Proc. Zool. Soc. London 124:493–499.

Klomp, H. 1970. The determination of clutch-size in birds, a review. Ardea 58:1–124.

Lack, D. 1954. The natural regulation of animal numbers. Clarendon Press, Oxford, England.

———. 1965. Evolutionary ecology. J. Anim. Ecol. 34:224–231.

MacArthur, R. H. and E. O. Wilson. 1967. The theory of island biogeography. Princeton Univ. Press, Princeton, New Jersey.

Martin, R. F. 1974. Syntopic culvert nesting of Cave and Barn swallows in Texas. Auk 91:776–782.

———. 1980. Analysis of hybridization between the hirundinid genera *Hirundo* and *Petrochelidon* in Texas. Auk 97:148–159.

——— and S. R. Martin. 1978. Niche and range expansion of Cave Swallows in Texas. Am. Birds 32:941–946.

——— and R. K. Selander. 1975. Morphological and biochemical evidence of hybridization between Cave and Barn swallows. Condor 77:362–364.

———, G. O. Miller, M. R. Lewis, S. R. Martin and W. B. Davis, II. 1977. Reproduction of the Cave Swallow: a Texas cave population. Southwestern Nat. 22:177–186.

Moreau, R. E. 1944. Clutch-size: a comparative study, with special reference to African birds. Ibis 86:286–347.

Myres, M. T. 1957. Clutch-size and laying dates in Cliff Swallow colonies. Condor 59:311–316.

National Oceanic and Atmospheric Administration. 1973. 1974. 1975. Climatological Data, Annual Summary, Texas. U.S. Dept. Commerce.

———. 1976. Climatological Summary, Brackettville, Texas. U.S. Dept. Commerce.

Ricklefs, R. E. 1969. An analysis of nestling mortality in birds. Smithson. Contrib. Zool. 9:1–48.

———. 1973. Fecundity, mortality, and avian demography. Pp. 366–447 *in* Breeding biology of birds (D. S. Farner, ed.). Natl. Acad. Sci., Washington, D.C.

Samuel, D. E. 1971. The breeding biology of Barn and Cliff swallows in West Virginia. Wilson Bull. 83:284–301.

Sinclair, A. R. E. 1978. Factors affecting the food supply and breeding season of resident birds and movements of Palearctic migrants in a tropical African savannah. Ibis 120:480–497.

Sokal, R. R. and F. J. Rohlf. 1969. Biometry. W. H. Freeman and Co., San Francisco, California.

von Haartman, L. 1971. Population dynamics. Pp. 391–459 *in* Avian biology, Vol. 1 (D. S. Farner and J. R. King, eds.). Academic Press, New York, New York.

TEXAS MEMORIAL MUSEUM AND DEPT. ZOOLOGY, UNIV. TEXAS AT AUSTIN, AUSTIN, TEXAS 78705. ACCEPTED 22 SEPT. 1980.

Wilson Bull., 93(4), 1981, pp. 519–530

HORNED LARK BREEDING BIOLOGY AT CAPE ST. MARY'S, NEWFOUNDLAND

Richard J. Cannings and William Threlfall

The Horned Lark (*Eremophila alpestris*) occupies a variety of barren habitats in Europe, North America (Vaurie 1959, Bent 1963) and Colombia. A number of studies have been made of this species in North America, mostly in the central part of the continent (Pickwell 1931; Garrett 1948; Beason 1970; Beason and Franks 1973, 1974; Boyd 1976). Little work has been done in the northern and eastern regions of the continent, however, other than that of Sutton and Parmelee (1955), who worked on Baffin Island, and Drury (1961) whose study area was Bylot Island.

STUDY AREA

We studied Horned Larks continuously during the 1976 breeding season (May–August) at Cape St. Mary's (46°47'N, 54°12'W), a headland at the southwestern tip of the Avalon Peninsula, Newfoundland and also made observations weekly in April and biweekly in February, March and September through November. In April 1977 a last visit was made.

Cape St. Mary's has a cool, temperate, maritime climate with long, relatively mild winters and short, cool summers (Meades 1973). Annual precipitation averages 150 cm, spread fairly evenly throughout the year. Fog is common, and occurred on about 60% of the days from May to August 1976, and on 24 days in July alone. Approximately 40% of the summer daylight hours in 1976 were foggy (visibility 25–100 m).

Temperatures from May to August varied from 0°C (13 June) to 23°C (12 July); daily maximums were usually between 10 and 15°C. Winds stronger than 20 km/h were common until late June and picked up again in late August. The severest storm of the summer (12–13 June) brought 70 mm of precipitation (rain and sleet) and winds up to 120 km/h.

The study area covered approximately 90 ha of headland heath extending back from the sea cliffs for 1–2 km. Using Meades' (1973) classification, the habitat consists of rocky barrens (*Diapensia* heath, *Polygonum viviparum* variant), hard ground heath (*Rhacomitrium* barrens and *Potentilla* heath), and local patches of soft ground heath. The tract is flat to somewhat undulating and treeless, except for a few very stunted balsam firs (*Abies balsamea*) growing in places protected from the wind. Lark territories were mapped by repeatedly flushing individuals or pairs and recording their positions with regard to established grid-points (see Cannings 1977). Territorial interactions, such as threat displays with flight chases, were also considered in the mapping of territories.

METHODS

Observations, including those of larks at their nests, were made with 8 × 30 binoculars and a 15–60× spotting scope. No blind was used. One male and 15 female larks were captured, individually color-banded, aged, sexed, weighed to the nearest 2 g (300 g Pesola scale) and measured (wing, culmen, tarsus, tail, hallux plus claw, first and ninth primaries). Each adult is referred to by a letter prefix (F—female, M—male) followed by a numeral (e.g., F3 was the third female captured).

As most nests found already contained eggs, dates of nesting starts were determined (and hence defined) by back-dating from hatching. Nests with eggs were usually checked several times daily to discover precise hatching times; those with young were visited at least once daily to measure the nestlings, in the same manner as adults. For individual identification, birds were marked on the tarsi with indelible ink at hatching and banded when 7 days old. Young larks were named by their nest number followed by another numeral, indicating the order of hatching when known (e.g., 34-1 was the first young to hatch in nest 34). Owing to the extreme wariness of adult larks when feeding young in the nest, direct observation of nest-feeding behavior was difficult. After the young had left, the nests were measured, collected and frozen. They were examined later to determine nest composition, dried (at room temperature) and weighed.

RESULTS AND DISCUSSION

The first lark seen near the study area in 1976 was a male on 4 April. In succeeding weeks larks appeared in increasing numbers on the study area from 8 April (5 birds) to 30 April. Tuck (*in* Peters and Burleigh 1951) noted that "large flocks" arrived in Argentia, Newfoundland (50 km north of present study area) in spring, a phenomenon not seen during the present study. Other workers (Pickwell 1931, Bannerman 1953, Boyd 1976) indicated that male larks normally return shortly before the females. We also noted this in Newfoundland in 1977, but not 1976, when many presumed pairs arrived at the same time. The larks seen between 14–18 April 1976 showed no territorial behavior and were not singing, perhaps due to wind conditions (30–70 km/h), which inhibit singing (Beason 1970). Larks seen on 3 April 1977 were singing and chasing each other. On arrival, larks stayed almost exclusively on the dry headland heath. Larks later nested along the gravel road that ran through the bogs.

General behavior: territories and courtship.—Twelve lark territories mapped in the study area (Fig. 1) ranged from 2.3 ha (E) –5.1 ha (A), with a mean of 3.5 ha. The territories were comparable in size to those found by Ryder (3.1 ha, at Argentia, Newfoundland, pers. comm.) and Pickwell (1931), but were larger than those of Beason and Franks (1974, 0.6–3.1 ha), Boyd (1976, 0.29–1.35 ha) and Lobachev and Kapitonov (1968, 0.15–0.25 ha), who worked with other subspecies. Territories were distributed in a linear fashion along the road, as male larks favored this area for dust-bathing, roosting and singing. Such an arrangement was also reported by Boyd (1976).

Territorial behavior (singing and the three types of hostile behavior described by Beason [1970]) was evident shortly after the larks arrived in April and was maintained until the last young left the nest in early August.

Territorial fights and chases were common from late April into July, becoming rare by the end of July. Aggressive behavior seemed to be more evenly distributed over the nesting season at Cape St. Mary's than pre-

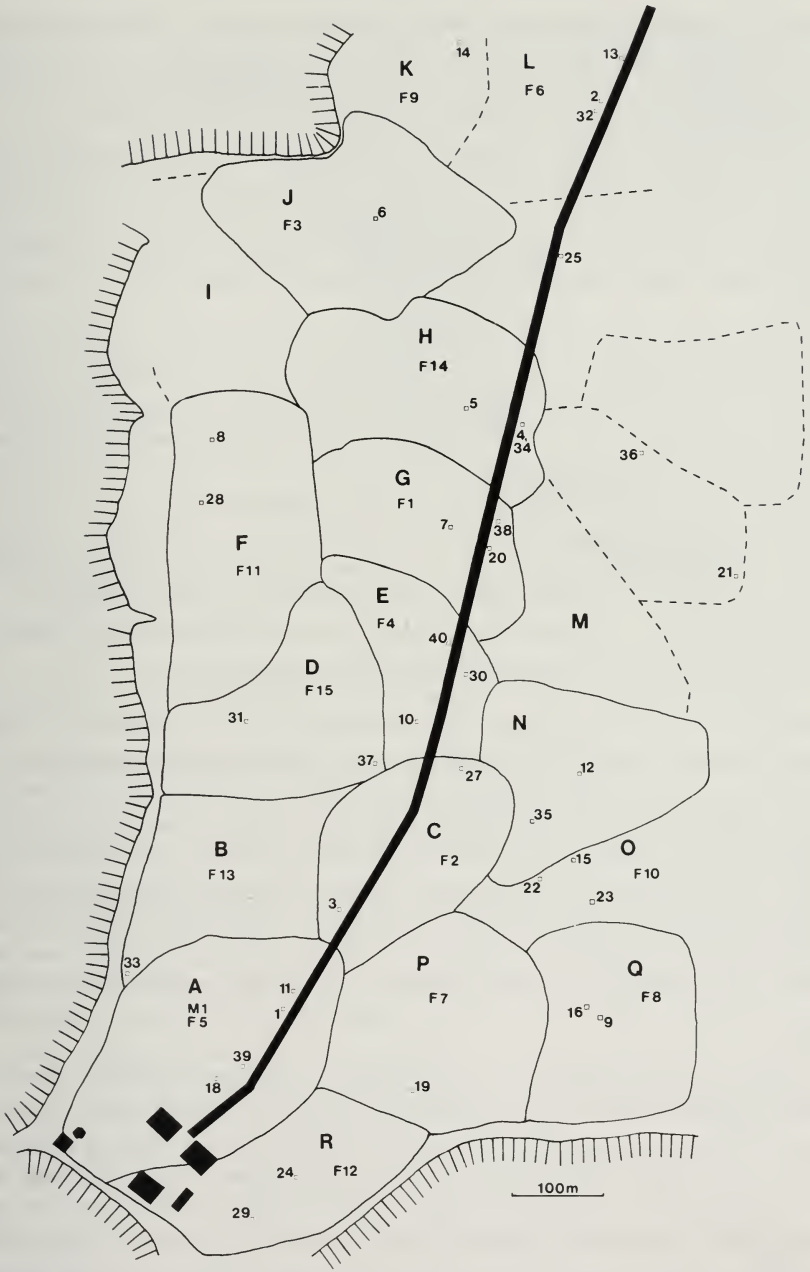


FIG. 1. Map of study area showing the boundaries of the mapped territories. The large single letter in each territory designates the territory, the letter-numeral groups (e.g., F12) indicate the resident adult larks. Nest locations are shown by the small open squares with the nest number. (Lighthouse complex located lower left.)

viously reported by Pickwell (1931) and other workers. With the large territories and very foggy weather at Cape St. Mary's, it may have been more difficult for male larks to patrol their boundaries, leading to many unchallenged trespasses and thus prolonging territorial disputes.

Trespassing was fairly common, as illustrated by the following: F13, observed gathering food for her nestlings in the immediate area of nest 18, 150 m from her territory, was completely ignored by F5 and M1, who were feeding young in nest 18 at the time. Larks from territories that did not take in the road sometimes dust-bathed on the road without being attacked.

Territoriality broke down as soon as the last brood left the nest and independent juveniles were not challenged on foreign territories. Young larks that had left their nest, but were still being fed, seemed to be kept within territorial limits by their parents. After 27 July small flocks of unbanded larks were common on the study area, and little or no agonistic behavior was noted between them and the resident larks.

Most agonistic behavior observed in the larks was restricted to male vs male confrontations. On only five occasions were females involved in this type of behavior, with hostilities being directed at other females, in a manner similar to—though not so frequent—as that described by Tinbergen (1939) for Snow Buntings (*Plectrophenax nivalis*).

Courtship displays were seen nine times, but copulation never followed any of those seen. The male approached the female with body held low to the ground, wings drooping and quivering, then bowed and fanned the tail. When the male stretched and held his head high, the black breast feathers were usually raised, enlarging the breast patch. Males attempted to mount females several times, but each time she side-stepped or fended him off with a kick. Often the female ran at the male as he approached. The similarity of the invitatory display (see Beason and Franks 1974) to dust-bathing was demonstrated in instances where males attempted to mount dust-bathing females. No male-female chases were seen that were definitely referable to the "sexual chase" as described by Beason and Franks (1974).

Nesting, eggs, incubation and hatching.—In Newfoundland, Horned Larks usually begin nesting between mid-May and early June; second broods, if any, occur in July and early August (Fig. 2). Nesting behavior was noted from 13 May (nest building) until 8 August, when the young left the last nest. The earliest known nesting date for the island can be extrapolated from a 3-week-old juvenile collected in St. John's 26 May 1968; this bird must have come from a nest begun around 24 April. The latest nesting date is Tuck's report of essentially flightless young at Argentia on 11 September 1947 (Peters and Burleigh 1951).

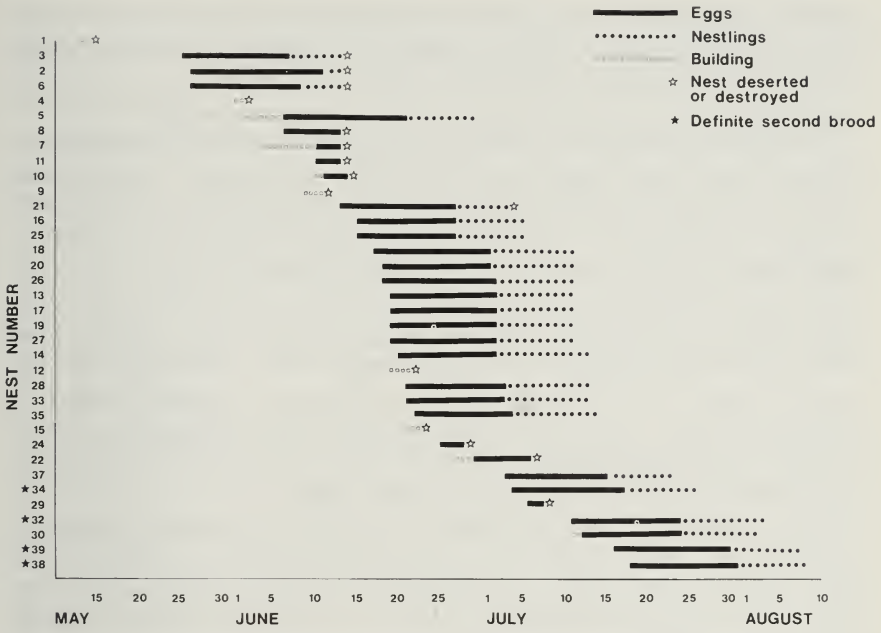


FIG. 2. Nesting phenology of Horned Larks in 1976 at Cape St. Mary's.

Nesting starts occurred from about 25 May until 11 June. A severe storm on 12–13 June, however, destroyed all three nests with young, and caused desertion of 4 of 5 nests with eggs. Three nests found after the storm (nests 16, 21, 25) were probably built before 12 June, and may have survived the storm because incubation had not begun. The earliest known second brood was started on 4 July (nest 34), in territory H, where one of the few nests to survive the storm was located. Three of the later nests (32, 38, 39) were second broods in territories where nests had not survived the storm.

Only the female built the nest, usually in the morning. The site was located in a depression dug in the ground, or in a tight mat of vegetation—crowberry (*Empetrum* sp.), lichen (*Cladonia* spp.) and/or moss (*Rhacomitrium lanuginosum*). Nests consisted of a grassy cup which was usually lined with a softer material (feathers or wool). Most had a small area of pebbles, or dried mud (paving) next to them. Vegetation cover associated with nest-sites is given in Cannings (1977). Nine of 31 nests examined were located within 50 cm of bare ground, and in the territories which contained the road, 15 of 18 nests were found within 10 m of the road, recalling Pickwell's (1931) earlier observations. Three nests were

located in cinnamon fern (*Osmonda cinnamommea*)—American burnet (*Sanguisorba canadensis*) habitat, but none were found in moist habitat, as they were by Verbeek (1967). While the female built the nest, the male was usually nearby, feeding, singing and chasing trespassers.

The mean dry weight of 31 nests was 16 g (range = 7–33 g), with the nests having a mean outer diameter of 99 mm (N = 26, range = 65–135 mm, some nests being asymetrical) and a mean inner diameter of 71 mm (N = 28, range = 55–85 mm). There was no significant variation in nest size or composition throughout the summer, contra Pickwell (1931).

Most nests were protected by vegetation on the windward side (N = 15, mean height of protection = 92 mm, range = 5–130 mm), with the open side facing west to northeast. The distribution of the directions was non-random, based on the Rayleigh test for randomness around a circle (r = 0.4142, $P < 0.05$). This bias in nest placement was probably due to the fact that the prevailing winds were from the southwest, and strong winds were most often from the quadrant south to east.

Nests were constructed primarily of grass, mostly *Deschampsia flexuosa*, with some lichens, rootlets, moss, leaves, feathers, small twigs and paper. Most of the lichens (predominantly *Cladonia* spp.) and mosses were on the outside of the grass cup, and were perhaps used to level the nest cup dug in the ground before the main grass structure was built. Seabird feathers were present in all nests examined, and wool in more than 50% of them. The only soft plant materials used in nest linings were leaves of the northern honeysuckle (*Lonicera villosus*) and down from willow (*Salix Uva-ursi*) catkins.

Dubois (1935), Beason and Franks (1974) and Boyd (1976) all noted that during Horned Lark nest construction an area of "pavings" (small pebbles and mud) was usually placed on one side of the nest. Dubois (1935) believed that the pavings served to cover and camouflage the dirt excavated from the nest cup, a view with which Beason and Franks (1974) and Boyd (1976) concurred and which is supported by our observations. In nest cups made in the mat of *Empetrum* no dirt was thrown out beside the nest. Seven of 15 nests built in this habitat had no trace of paving, while only 1 of 15 nests built in short grass on the roadside, or in gravelly habitat, had no trace of paving. This difference (7/15 vs 1/15) is significant (χ^2 = 6.136, $P < 0.05$). This may, however, simply reflect a closer supply of paving material at the roadside nests. The nest building time noted in this study approximates that noted by Beason (1970). The most rapidly built and loosely constructed nest of those observed in the present study was a simple cup dug in the *Empetrum nigrum* mat, with a few grass stems, feathers and bits of willow down. It contained an egg the day after discovery. Nests 1, 9, 12, 15 and 40 found in the study area were incomplete

and apparently deserted early. Beason (1970) reported a female building two nests simultaneously, a phenomenon that we also found once; the female used one nest, later finishing the second nest in which she raised a second brood.

Renesting after nest destruction or desertion was recorded nine times. The time interval between nest abandonment and renesting (measured to the day the first egg was laid) averaged 5.8 days (N = 5, range = 4–8). The interval between the time the young left a successful nest and the initiation of a second brood averaged 4.0 days (N = 4, range = 0–7). The zero value came from territory L, where F6 laid the first egg in nest 32 on the same day the young left her nest 13. The second nest must have been built while she was feeding the young in the first. Four of 16 pairs of larks raised two successful broods.

Eggs were usually laid before 05:00, at a rate of one per day until completion of the clutch. In contrast, Boyd (1976) found eggs were often laid every other day in very early nests. Clutch-sizes of 26 nests varied from 2–4 (1 [2], 16 [3], 9 [4]), with a mean of 3.3 ± 0.6. A significant increase in clutch-size over the breeding season was noted, with a mean clutch-size of 3.0 in 10 nests begun before 15 June. That of 16 nests begun after 15 June was 3.5 ($t = 2.48$, $P < 0.05$). Of eight females for which two or more nesting attempts were recorded, four had two clutches of three, and four contained a first clutch of three and then a clutch of four. Only one first nest contained a clutch-size of four, and it was one of the latest first nests. This trend to increased clutch-size in passerines, over the breeding season, is well documented (e.g., Delius 1965).

Incubation, by the female only, usually began after the last egg was laid, although in eight nests it began with the penultimate egg. The latter led to asynchronous hatching, with chicks emerging over a 3-day period in one instance. In only four nests was the incubation period determined, averaging 12.3 days (11, 11, 13, 14 days, respectively). Pickwell (1931) reported an 11-day incubation in this species, although it may be longer in inclement weather (Boyd 1976).

Posthatching behavior.—The chicks, on hatching, were covered with a long buff down, as noted by Dubois (1935), Wetherbee (1957) and Beason (1970), which enabled them to blend into the background when they crouched on being disturbed. The young were brooded by the female for the first few days after hatching, and every night until they left the nest.

Both parents normally fed the chicks, although in one case a female raised two broods alone. The lack of help in the latter case (whereabouts of the male was unknown) did not appear to affect nestling growth, although one late-hatcher probably was not fed and died 5 days after hatching. The mid-afternoon mean feeding rate of nestlings, in one nest, was

once every 3.0 min vs a mean of 5.5 min noted by Pickwell (1931), and the extraordinary case noted by Levy (1920) where two adult larks fed eight young in one nest once every minute.

Forty-seven nestlings of known age were measured, usually daily, for a total of 302 nestling-days of measurement. The results are shown in Fig. 3. Growth rate (weight increase) was analyzed using the graphical method of Ricklefs (1967). Assuming an asymptote weight of 34 g, nestling overall growth rate was 0.543, which is slightly higher than the 0.464 calculated from Pickwell's (1931) data reported by Ricklefs (1968), but very near the mean values given for ground-nesting passerine species by Ricklefs (1967). As noted in other ground-nesting passerines the legs and feet developed rapidly, this being highly advantageous in allowing early nest-leaving and thus avoidance of nest predation (Burns 1921).

The nestlings in the early nests (those which perished in the storm of 12–13 June) grew much more slowly than those from later nests, probably due to a scarcity of food and the poor weather during this period. Nestlings in the majority of nests were fed equally, despite competition for food from conspecifics. However, in at least four nests the last hatched chick grew more slowly than its nest-mates. In one case a female was seen to feed two chicks in a nest while at the same time the male fed a third chick and a juvenile from the previous brood.

The nestling period (time between hatching and fledging) averaged 9 days (5 nests, 8 days; 26 nests, 9 days; 5 nests, 10 days). The chicks left during the daylight hours, often over a period of 2–3 days. One or 2 days after leaving the nest the young could not fly, but hopped clumsily, using their wings for balance. Their main predator-avoidance behavior was crouch-concealment (Pickwell 1931). As their locomotory ability increased, the young larks began to run along behind their parents, giving a distinctive *breet* call, which was used for several weeks after nest-leaving and which was easily distinguishable from the adult *weet* call. After 3 or 4 days out of the nest, the young could fly a few meters, and by 14 days of age they could fly distances of 50 m repeatedly without any noticeable tiring. If a juvenile of this age was forced to fly several times consecutively, its parents accompanied it, giving loud alarm calls, and near territorial boundaries the adults seemed to try to herd the young bird back into the home territory. Young larks began to be independent of their parents when they were about 3 weeks old, at which time they were able to fly strongly. Although juveniles as old as 26 days were seen with their parents, an equal number of birds this age were observed feeding by themselves in the territory of another pair of adults. Young larks fed primarily on pink crowberries (*E. eamesii*) after reaching independence.

The first small flocks, indicative of post-breeding activity, were seen in

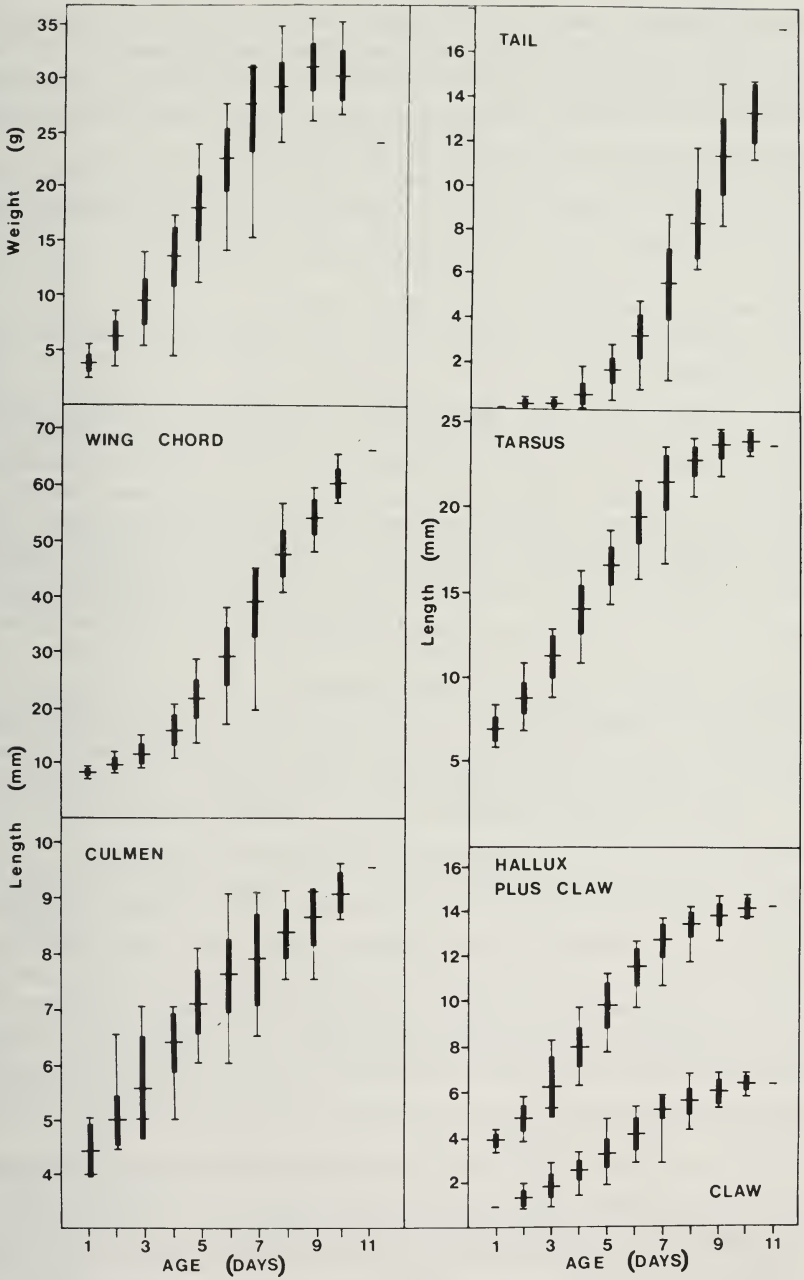


FIG. 3. Growth rates of nestling Horned Lark chicks. Day 1 represents the day the chicks hatched. Each bar shows the mean, standard deviation and range of measurements.

late July. On 27 July, a flock of 13 Horned Larks (five males, two females and six juveniles) was seen on the study area. These were probably not local larks, since none of the birds were banded. By early August, when most local juveniles were about 1 month old, several small mixed flocks of local young and female larks were seen feeding together.

Horned Larks leave their breeding grounds in Newfoundland in late September and October, with a few remaining until early November (Peters and Burleigh 1951). We saw small flocks of larks (3–35 individuals) on the study area through September in 1976, and had seen larks until mid-November in 1975 (during a seabird census).

The overall breeding success (number of young leaving nest per eggs laid) of Horned Larks at Cape St. Mary's in 1976 was 58.8% (N = 24 nests, 80 eggs), this figure being high when compared to others in the literature. The mean number of fledglings produced by each breeding pair during this study was 4.0 (N = 12, range = 0–7). The birth rate (fledgling/adult/season) was 2.0, with a replacement rate of approximately 67%.

Predation probably accounted for 43% of all egg and nestling loss, with ermines (*Mustela erminea*), mink (*M. vison*), red fox (*Vulpes vulpes*), meadow voles (*Microtus pennsylvanicus*), shrews (*Sorex cinereus*) and a domestic cat (*Felis domestica*) being regularly present in the study area. Ravens (*Corvus corax*) were also present, but seemed to confine their nest-robbing activities to adjacent seabird colonies.

Inclement weather (the storm of 12–13 June) accounted for 28% of egg and nestling losses. All nestlings known to be present died at this time and nest 7, which contained three eggs, was deserted. Three other nests (8, 10 and 11) suffered predation during or shortly after the storm. Nest desertion occurred at two nests after the incubating female had been captured on the nest for banding. Only 1 of 86 eggs observed through the normal hatching period proved to be infertile, and one egg (containing a well-developed embryo) in nest 16 failed to hatch after it was pushed up onto the nest lip, apparently by the incubating female. An egg was also found just outside the cup of nest 8. It was marked and returned to the nest, but a predator destroyed the nest before the eggs hatched. Beason and Franks (1974) also reported that females took no notice of eggs outside the nest cup. Starvation caused the death of at least three late-hatching nestlings at Cape St. Mary's.

Food and feeding.—Horned Larks usually fed by probing the ground vegetation with their bills, searching for arthropods, berries and seeds. They sometimes interrupted this ground-probing to run quickly after a low-flying wasp or moth. On 5 August, F3 was seen repeatedly flying after moths in the manner of a flycatcher. Larks also ate bog cranberries (*Vaccinium oxycoccos*), pink crowberries, large black ants, moth caterpillars

and adults, beetles, craneflies (Tipulidae) and spiders. Nestlings were fed arthropods almost entirely, whereas adults, especially early in the season, ate more seeds, berries and small leaves. This is consistent with the findings of McAtee (1905 *fide* Beason 1970) and Boyd (1976). All birds examined, except the nestlings from nest 2 (which were only 1 day old at death), had some grit in their gizzards. Almost half (8/18) of the gizzards from birds collected at Cape St. Mary's contained small bits of mollusc shell.

SUMMARY

The breeding biology of the Horned Lark (*Eremophila alpestris*) was studied during the 1976 breeding season at Cape St. Mary's, Newfoundland. Territorial behavior was investigated, and territories were subsequently mapped to determine their size (2.3–5.1 ha, $\bar{x}$ = 3.5 ha).

Nesting phenology was studied in detail. Nests were weighed, measured and their composition determined; they were so placed as to be protected on the windward side. Clutch-sizes of early and late nests were compared (early 3.0 eggs, late 3.5 eggs, overall mean 3.31 eggs). Forty-seven nestlings were measured to calculate growth curves for weight and other body variables. Breeding success (58.8%), incidence of renesting, and the mean number of fledglings (4.0) produced by each pair were calculated. Causes of egg and nestling loss were analyzed, and predation determined to be the most important factor. About 25% of the breeding pairs raised two successful broods.

ACKNOWLEDGMENTS

We wish to thank O. L. Austin, Jr., G. Brassard, S. Cannings, J. Rice, R. A. Ryder, P. Scott and the late L. M. Tuck for their help and advice during the course of this study. This manuscript was written while the junior author was a Visiting Professor in the College of Veterinary Medicine, University of Florida, Gainesville. This work would not have been possible without generous support from the National Research Council of Canada.

LITERATURE CITED

Bannerman, D. A. 1953. The birds of the British Isles, Vol. 2. Oliver and Boyd, London, England.

Beason, R. C. 1970. The annual cycle of the Prairie Horned Lark in west central Illinois. M.Sc. thesis, Western Illinois Univ., Macomb, Illinois.

——— and E. C. Franks. 1973. Development of young Horned Larks. Auk 90:359–363.

——— and ———. 1974. Breeding behavior of the Horned Lark. Auk 91:65–74.

Bent, A. C. 1963. Life histories of North American flycatchers, larks, swallows, and their allies. U.S. Natl. Mus. Bull. 179.

Boyd, R. L. 1976. Behavioral biology and energy expenditure in a Horned Lark population. Ph.D. thesis, Colorado State Univ., Fort Collins, Colorado.

Burns, F. L. 1921. Comparative periods of nestling life of some North American nidicolae. Wilson Bull. 33:4–15.

Cannings, R. J. 1977. The breeding biology of the Horned Lark (*Eremophila alpestris* L.) at Cape St. Mary's, Newfoundland. M.Sc. thesis, Memorial Univ., St. John's, Newfoundland.

Delius, J. D. 1965. A population study of skylarks, *Alauda arvensis*. Ibis 107:466–492.

Drury, W. H. 1961. Studies on the breeding biology of Horned Lark, Water Pipit, Lapland Longspur, and Snow Bunting on Bylot Island, Northwest Territories, Canada. Bird-Banding 32:1–46.

Dubois, A. D. 1935. Nests of Horned Larks and longspurs on a Montana prairie. Condor 27:56–72.

Garrett, M. L. 1948. The life history of the Prairie Horned Lark. M.Sc. thesis, Ohio State Univ., Columbus, Ohio.

Levy, F. 1920. An unusual Horned Lark family. Bird-Lore 22:85–86.

Lobachev, Y. S. and V. I. Kapitonov. 1968. Ecology of the Horned Lark (*Eremophila alpestris albigula* Bp.) in the Karzhantau Mountains (Western Tien-Shan). Byull. Mosk. O-va. Ispyt. Prir. Otd. 73:17–25.

Meades, W. 1973. A phytosociological classification of the Avalon Peninsula heath, Newfoundland. M.Sc. thesis, Memorial Univ., St. John's, Newfoundland.

Peters, H. S. and T. D. Burleigh. 1951. The birds of Newfoundland. Dept. Nat. Resour., St. John's, Newfoundland.

Pickwell, G. B. 1931. The Prairie Horned Lark. St. Louis Acad. Sci. Trans. 27:1–153.

Ricklefs, R. E. 1967. A graphical method of fitting equations to growth curves. Ecology 48:978–988.

———. 1968. Patterns of growth in birds. Ibis 110:419–451.

Sutton, G. M. and D. F. Parmelee. 1955. Nesting of the Horned Lark on Baffin Island. Bird-Banding 26:1–18.

Tinbergen, N. 1939. The behavior of the Snow Bunting in spring. Trans. Linn. Soc. N.Y. 5:1–91.

Vaurie, C. 1959. The birds of the Palearctic fauna. H.F. and G. Witherby, London, England.

Verbeek, N. A. M. 1967. Breeding biology and ecology of the Horned Lark in alpine tundra. Wilson Bull. 79:208–218.

Wetherbee, D. K. 1957. Natal plumages and downy pteryloses of passerine birds of North America. Am. Mus. Nat. Hist. Bull. 113:343–436.

Dept. Biology, Memorial Univ. of Newfoundland, St. John's, Newfoundland A1B 3X9 Canada. Accepted 17 Feb. 1981.

Wilson Bull., 93(4), 1981, pp. 531–537

ASPECTS OF THE BREEDING BIOLOGY OF A SUBTROPICAL ORIOLE, *ICTERUS GULARIS*

Barbara Yohai Pleasants

In this paper I describe several aspects of the breeding biology of Lichtenstein's Oriole (*Icterus gularis*). Similar to other subtropical and tropical orioles *I. gularis* is sexually monomorphic, is resident throughout the year and is found in wooded habitats. Although breeding populations of *I. gularis* are established in the U.S., little information is available for this species in any portion of its range. There are brief discussions of its life history (Bent 1958, Oberholser 1974) and a description of nest-building (Sutton and Pettingill 1943).

METHODS

I. gularis occurs from the Rio Grande Valley southward through eastern Mexico to Guatemala. This study was conducted at the northern limit of the range of the species, on the Santa Ana National Wildlife Refuge near Alamo, Hidalgo Co., Texas. The area is warm and relatively dry, with a mean annual rainfall of 45 cm (Fleetwood 1973). The refuge consists of 800 ha covered, in most sections, by primarily evergreen, dry, subtropical forest. The land surrounding the refuge has been cleared for agriculture, leaving Santa Ana as an island of natural habitat. The commonest trees are Texas ebony (*Pithecellobium flexicaule*), tepeguaje (*Leucaena pulverulenta*), elm (*Ulmus* spp.) and ash (*Fraxinus* spp.). Below the canopy is a dense understory of shrubs and thorny vines.

Almost all observations were made from 16 May–6 June 1974. Two brief visits during March 1977 and March 1978 provided additional information. I found 19 nests (two were outside the refuge boundaries) during the 1974 study and at eight of these I collected data on various aspects of parental behavior (Pleasants 1977). Most nests were found while clutches were being incubated. Once located, a nest was checked daily and extensive observation began when the eggs hatched. I then observed the activity at each nest as often as possible for the remainder of the study. Most nests were observed on three or more different days (Table 1). I obtained information on type of food brought to young, frequency of feeding of nestlings and adult behavior in the vicinity of the nest. A total of 1744 min of these observations were made at the 8 suitable nests (Table 1). A single observation session lasted 30–60 min; generally these sessions occurred between 07:30 and 12:00 or between 15:00 and 20:00 when the adults were most active. Because of the inaccessible nature of the nests, no data on contents could be obtained. Locations of all nests were plotted on a map of the refuge.

RESULTS AND DISCUSSION

Characteristics of breeding adults.—All adults seen at nests were in full adult plumage (orange and black). Temperate oriole populations, on the other hand, often have significant proportions of breeding first-year males (pers. obs., Rising 1970, Sealy 1980). These first-year males have not attained adult male appearance and resemble females in coloration. Adult

Table 1
Observation Periods for *Icterus gularis* During Nestling Stage, 1974

Pair/nest	Dates of observation	No. of observation periods	Total time observed (min)
1	18–29 May	10	400
2	21 May–4 June	10	585
3	20 May–4 June	4	180
4	31 May–5 June	3	121
5	29 May–6 June	3	134
6	31 May–3 June	2	124
7	1 June–4 June	3	110
8	24–28 May[a]	4	90

[a] Brood apparently destroyed between 24 and 25 May.

mortality in tropical passerines is low (Cody 1971); breeding territories and pair bonds may be permanent (Orians 1969). Young birds will find it difficult to enter the breeding population under such circumstances. In the tropical Rufous-collared Sparrow (*Zonotrichia capensis*), young birds remain on the permanent territories of adults waiting for vacancies to occur in the breeding population (Smith 1978). Young *I. gularis* may employ the same strategy. Activities near the nest of a widowed female *I. gularis* (nest 7) may aid in understanding the process of entry into the breeding population by young birds. (The presumed mate of this bird was found dead on the road quite close to the nest.) She continued to feed the nestlings on her own for the remainder of my stay on the refuge (6 days). A male in immature plumage (yellow and black) was repeatedly seen in the vicinity of the nest. He never brought food to the nestlings and spent a good part of his time singing. I observed no interactions between him and the female.

Nests.—I. gularis builds a pendulous nest approximately 60 cm in length. The nest is situated on a branch tip 10 m or more above the ground, and is conspicuous (also see Sutton and Pettingill 1943). The trees selected as nest-sites are typically emergent above the canopy, so the nest is visible for some distance. Leaves of the preferred nest trees (legumes like *Pithecellobium*) are woven into the nest and the structure swings freely. Nine of 10 nests checked for placement were within the NW quadrant of the nest tree. The length of the nest makes it necessary for adults to land first on the upper part of the exterior and then maneuver to crawl head downwards into the bag itself. This delay facilitated my observation of individuals and of food items they carried for nestlings.

Nest-building takes up to 26 days in *I. gularis* (Oberholser 1974). This is in marked contrast to the 5–6 days temperate species (Northern Oriole [*I. galbula*], Hooded Oriole [*I. cucullatus*]) spend building their smaller nests (pers. obs.). This difference in nest-size and building period may be attributable to the permanent resident status of *I. gularis*, which allows the species more time to build a secure structure. Ricklefs (1969) suggested that tropical birds' more complex forms of nest construction are due to predation pressure. The length of *I. gularis* nests makes quick entry and exit by brood parasites or predators quite difficult. The structure of these nests is presumably the result of selection pressure to reduce egg and nestling mortality (see below, Behavior at nest).

Spacing system.—Mean nearest-neighbor distance for the 17 nests located within the refuge was 250 m (range 63–443 m, distances measured on map). Two other nests were located in small stands of trees outside the refuge boundary. During all the time I spent watching *I. gularis* from nest-building to fledging, I saw only one instance of aggression between pairs. These birds are solitary nesters with exclusive access to the food resources in the territories which surround their nests. Year-round residence may greatly lower the frequency of overt territorial defense. All-purpose territoriality (Type A) is predicted for a species nesting in a large patch of relatively uniform habitat, such as a forest (Brown 1964, Horn 1968). This contrasts with the more colonial spacing system characteristic of Northern Orioles breeding in small patches of riparian woodland surrounded by habitat unsuitable for nesting (Pleasants 1979).

Behavior at nest.—Compared to *I. galbula*, *I. gularis* is a quiet species. Males sing and whistle softly, usually near the nest, while females rarely sing. The chattering sound so common in Northern Orioles is lacking. Instead, both adults utter a soft "nasal" call as a contact note and when arriving at the nest with food.

Nestlings and fledglings of *I. gularis* also tend to be quiet. None of the fledglings of two broods made any sounds that I heard. In contrast, I could easily locate fledgling *I. galbula* by their constant begging calls. This interspecific difference in behavior of young may reflect differences in the causes of fledgling mortality; predation is potentially a more significant factor for *I. gularis*.

I found that *I. gularis* adults produced a characteristic call as their young approached fledging. This two-note call, similar to the beginning of full song, was not heard earlier in the nesting cycle. Parents continued to use this call when approaching young even after the young had fledged.

Feeding.—Like most icterids, orioles are generalists with regard to diet. Although primarily insectivorous, they will also take nectar and fruit. I observed no *I. gularis* young being fed fruit and saw an adult eating fruit

TABLE 2
FOOD ITEMS BROUGHT TO NESTLINGS

Food item	No. items	% total
Grasshoppers (Orthoptera)	42	33
Caterpillars and other larvae	36	29
Walkingsticks (Phasmidae)	26	21
Other insects	4	3
Unidentified	18	14

only once. Oberholser (1974) states that adults eat hackberries (*Celtis* sp.) and figs (*Ficus* sp.). Table 2 lists food items brought to nestlings by *I. gularis* parents.

Data on the rate at which nestlings were fed were gathered at all nests which had young during the study. Fig. 1 shows the negative relationship between age of nestlings and the interval between successive feedings by adults (Spearman rank correlation, $r = -0.719$, $P < 0.01$). During the first two days post-hatching, feeding intervals are substantially longer than on succeeding days and longer than intervals for *I. galbula* of similar age (Pleasants, unpubl.). From the third day on, feeding intervals for *I. gularis*

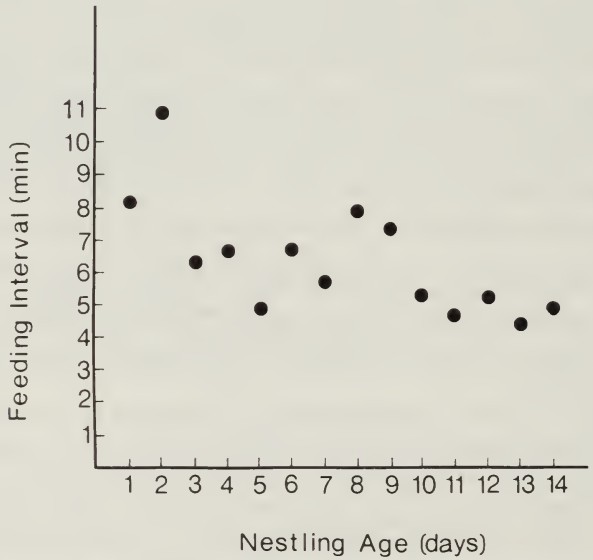


FIG. 1. Feeding interval as a function of nestling age. Each point is based on data for 1–4 pairs.

fall within the range of intervals I found for seven populations of *I. galbula*. Interestingly, feeding intervals for *I. galbula* do not decrease as nestlings get older. (These differences between species will be discussed further in a separate paper.) The widowed female, whose nestlings were of unknown age, brought food at intervals from 4.5–5 min on three successive days. Surprisingly, these intervals correspond to those for nestlings with two parents.

Skutch (1943) suggested that tropical birds feed their young less often than their temperate relatives in order to reduce chances of detection by predators. For *I. gularis* this may be true when nestlings first hatch, but for the bulk of the nestling period food availability and demands of growing young preclude such a strategy.

Interactions with other species.—The Bronzed Cowbird (*Molothrus aeneus*) is abundant on the refuge, its numbers having increased in recent years. Parasitism by this cowbird is believed responsible for the disappearance of Hooded Orioles from the refuge (Oberholser 1974). I often saw groups of 3–5 cowbirds near *I. gularis* nests, particularly those in which eggs had not yet hatched. During a 30-min period, one nest was approached by three cowbirds shortly after the orioles had left the tree. The cowbirds remained for 15 min despite an attempt by the returning male oriole to drive them away. During a later 60-min period of observation at the same nest 1–3 cowbirds approached five separate times, often landing directly on the nest. A female cowbird entered the nest and remained inside for 4.5 min. This oriole pair was probably at the egg-laying stage when this occurred; nest-building was complete and incubation began a few days later.

Orioles often nest near kingbirds (*Tyrannus* spp.) or other large tyrannids, according to anecdotal accounts (Bent 1958). Many flycatcher species are aggressive, vociferous birds that readily attack predators larger than themselves. On the Santa Ana Refuge the Kiskadee Flycatcher (*Pitangus sulphuratus*) is the most conspicuous large flycatcher. Four of 10 *I. gularis* nests were placed within 3–4 m of kiskadee nests and one of the four was also close to the nest of a pair of Tropical Kingbirds (*T. melancholicus*). This suggests the existence of a nesting association from which the orioles gain protection as a result of the presence of large tyrannids.

Several observations support the protection hypothesis. One pair of orioles was reluctant to approach the nest with food when I first began my observations. Instead, a bird would perch in a nearby tree with food items visible in its bill. After the return of a kiskadee to its own nest about 3 m away, the oriole would fly to its nest and feed the young. When feeding young, each kiskadee adult usually waited near the nest for its mate to return before leaving on its next foraging trip, so that at least one adult

was in the vicinity of the nest. In contrast, orioles would often leave together on foraging trips. More importantly, kiskadees do chase other birds from oriole nests. Bronzed Cowbirds were chased on four occasions; chachalacas (*Ortalis vetula*) and an unidentified dove were also chased. One kiskadee, nesting 2 m from the widowed female oriole, chased the young male oriole that had taken up residence on her territory. The Tropical Kingbirds nesting near pair #2 chased Great-tailed Grackles (*Quiscalus mexicanus*)—known predators on eggs and nestlings (Bent 1958). If this is an actual association between orioles and large tyrannids, rather than chance close proximity, there should be selection by orioles of nestsites near Kiskadee Flycatchers. Kiskadees appear to begin nest-building before the orioles do (Pleasants, pers. obs. March 1977).

SUMMARY

Lichtenstein's Orioles were studied for three weeks during the breeding season on the Santa Ana National Wildlife Refuge in southern Texas in 1974. I located 19 nests and made extensive observations at eight of them. All breeding birds were in full adult plumage. A first-year male was repeatedly seen in the vicinity of a widowed female with young and the possible significance of this is discussed. Nests are large, pendulous structures, situated in emergent leguminous trees and generally located in the NW portion of the tree. Food items brought to nestlings are listed. The mean interval between successive feedings decreases as nestlings get older. There may be a nesting association between these orioles and large tyrannid flycatchers which would benefit the orioles by protection from brood parasites and predators.

ACKNOWLEDGMENTS

The work reported on here was part of a doctoral dissertation submitted to the University of California, Los Angeles. I would like to thank personnel of the Santa Ana National Wildlife Refuge, particularly Wayne Shifflett and Cruz Martinez, for sharing their knowledge of refuge birds. John M. Pleasants provided invaluable field assistance. M. L. Cody, H. A. Hespenheide, J. M. Pleasants and reviewers for this journal offered useful criticism of various drafts of this manuscript.

LITERATURE CITED

Bent, A. C. 1958. Life histories of North American blackbirds, orioles, tanagers and allies. U.S. Natl. Mus. Bull. 211.

Brown, J. L. 1964. The evolution of diversity in avian territorial systems. Wilson Bull. 76:160–169.

Cody, M. L. 1971. Ecological aspects of reproduction. Pp. 461–512 *in* Avian biology, Vol. 1 (D. Farner and J. King, eds.). Academic Press, New York, New York.

Fleetwood, R. J. 1973. Plants of Santa Ana National Wildlife Refuge. U.S.D.I., Fish and Wildl. Serv.

Horn, H. S. 1968. The adaptive significance of colonial nesting in the Brewer's Blackbird. Ecology 49:682–694.

Oberholser, H. C. 1974. The bird life of Texas. Univ. Texas Press, Austin, Texas.

ORIANS, G. H. 1969. The number of bird species in some tropical forests. Ecology 50:783–801.

PLEASANTS, B. Y. 1977. Ecological factors affecting the breeding dispersion patterns of some North American orioles (*Icterus*). Ph.D. thesis. Univ. California, Los Angeles, California.

———. 1979. Adaptive significance of the variable dispersion pattern of breeding Northern Orioles. Condor 81:28–34.

RICKLEFS, R. E. 1969. The nesting cycle of songbirds in tropical and temperate regions. Living Bird 8:165–175.

RISING, J. D. 1970. Morphological variation and evolution in some North American orioles. Syst. Zool. 19:315–351.

SEALY, S. G. 1980. Breeding biology of Orchard Orioles in a new population in Manitoba. Can. Field-Nat. 94:154–158.

SKUTCH, A. F. 1949. Do tropical birds rear as many young as they can nourish? Ibis 91:430–455.

SMITH, S. M. 1978. The "underworld" in a territorial sparrow: adaptive strategy for floaters. Am. Nat. 112:571–582.

SUTTON, G. M. AND O. S. PETTINGILL, JR. 1943. The Altamira Oriole and its nest. Condor 45:125–132.

DEPT. ZOOLOGY, IOWA STATE UNIV., AMES, IOWA 50011. ACCEPTED 22 JUNE 1981.

Wilson Bull., 93(4), 1981, pp. 538–540

GENERAL NOTES

An example of a hybrid Green Jay × Blue Jay.—While attempting to secure fledgling Blue Jays (*Cyanocitta cristata*) for use in a behavioral study, Dellinger learned that there was a hybrid between a Green Jay (*Cyanocorax yncas*) and a Blue Jay on exhibit at the Zoological Park in Fort Worth, Texas. She visited the park on 18 September 1977, and learned that the jay was over 12 years old at the time, having hatched on 17 June 1965.

The hybrid was the result of a mating between a male Green Jay and a female Blue Jay during the spring of 1965. The female, a locally hand-reared bird hatched in 1964, was obtained from a bird rehabilitator as a possible mate for the Green Jay. There was no record of where the male was obtained. The mating produced two clutches, the first of which failed. The second clutch comprised three eggs laid on 30, 31 May and 1 June; only one young hatched successfully. Soon after the young was taken from its parents and hand-reared. The hybrid was placed as a juvenile in an outdoor cage holding other jays.

The hybrid died on 28 January 1978, and was donated to the vertebrate collection at the University of Texas at Arlington (number UTA 730). Both skin and carcass were preserved. The specimen proved to be a male weighing 104 g, with little fat, having an enlarged left testis, yellowish-orange irides, and with bill and fleshy parts of the mouth black. The lower mandible showed a slight deformity. Measurements were as follows: total length 320 mm, wing 129 mm, tail length 141 mm, tarsus 35.5 mm, culmen 21 mm.

Unfortunately, no behavioral notes were kept on the hybrid from initial fledging in 1965 to 18 September 1977. Zoo personnel informed us that at times the hybrid was housed with Blue and Green jays. When Dellinger observed the bird in September 1977, it was with a Scrub Jay (*Aphelocoma coerulescens*) and eight other species. From late October 1977 until its death, the hybrid was housed with two hand-reared, first year Blue Jays, and may have been forming a pair bond with one, as food exchange was noted several times.

On 18 September and again on 20 October 1977, Dellinger heard the hybrid give a call much like that of a typical Blue Jay. It responded to wild Blue Jays outside by flying to the side of the cage, clinging to the wire and calling *jay*. The hybrid also sang quietly on 20 October, a behavior of frequent occurrence according to zoo personnel.

Fig. 1 shows the morphological features of the hybrid. Blue, typical of Blue Jays, was dominant; Green Jay colors were generally absent. The forehead and crown were primarily white with blue tips and edges; feathers obscuring the nares were blue with black tips; the lores and auriculars were black; and the malar region was blue with black in the adjoining areas. Small patches of blue were present above and below the eyes, but feathers immediately in front of and behind the eyes were black. The chin and throat were black mottled with blue. The upper breast was also black and separated from the white belly by a transition area of blackish-blue. The sides of the breast were bluish-gray. The undertail coverts, femorals and crurals were white, the back and uppertail coverts blue. The nape was blue mixed with white and closely resembled that of a Blue Jay. The alulae and primaries were blue. The blue secondaries and tertiaries were broadly tipped with white; the upper primary coverts were all blue and the upper secondary coverts were blue, tipped with white. The upper, middle and lesser wing coverts were also blue with the marginals showing some white on the inner webs. Faint barring was apparent on the largest alular feathers, some secondaries, tertiaries and the upper greater secondary coverts. The underwing coverts were mostly white. The two central rectrices were blue; those adjoining were blue, tipped with white; and those outermost were mainly white. The barring of the tail, so characteristic of a true Blue Jay, showed only faintly.

Previous records of hybridization among jays in the wild include that of a White-tipped

FIG. 1. Captive hybrid Green Jay × Blue Jay.

Brown Jay (*Psilorhinus morio*) × Magpie Jay (*Calocitta formosa*) from western Chiapas, Mexico (Pitelka et al., Condor 58:98–106, 1956), and a Blue Jay × Steller's Jay (*Cyanocitta stelleri*) from Boulder, Boulder Co., Colorado (Williams and Wheat, Wilson Bull. 83:343–346, 1971).

Hardy and Raitt (abstract, Proc. 16th Int. Ornithol. Congr. 105, 1974) reported successful captive hybridization between a Yucatan Jay (*Cissilopha yucatanica*) and a San Blas Jay (*C. sanblasiana*), but, unfortunately, the young died at 24 days. In 1973, a Beechey's Jay (Purplish-backed Jay [*C. beecheii*]) was crossed with a Magpie Jay at the Arizona-Sonora Desert Museum in Tucson, Arizona, where, according to Gale Monson (pers. comm.), the hybrid is still alive and on display. He also stated that as an adult it shows more characteristics of the Beechey's Jay than of the Magpie Jay. It has the dark eyes of the latter, rather than the yellow eyes of the adult Beechey's Jay.

The possibility of the Green Jay and the Blue Jay occurring naturally together during the breeding season is remote, so that hybrids are not to be expected in the wild. In Texas, the Green Jay occurs locally throughout the Rio Grande Valley to Laredo, Webb Co., and to Falfurrias, Brooks Co., and occasionally north to Alice, Jim Wells Co., and sporadically north to San Antonio, Bexar Co. In winter, the Blue Jay is found as a straggler on Edwards Plateau just north of San Antonio and rarely in the Rio Grande Valley.

We should like to thank Jon C. Barlow, John Darling, John William Hardy, Ronald Kimbell, Terry C. Maxwell and Gale Monson for their comments and assistance in the preparation of this note.—Warren M. Pulich, *Dept. Biology, Univ. Dallas, Irving, Texas 75061* and Rebecca M. Dellinger, *P.O. Box 163, Duncanville, Texas 75116.* *Accepted 20 Oct. 1980.*

Wilson Bull., 93(4), 1981, p. 540

Dusky Seaside Sparrow feeds Red-winged Blackbird fledglings.—The endangered Dusky Seaside Sparrow (*Ammospiza maritima nigrescens*), restricted to small tracts of salt and brackish marsh near Titusville, Brevard Co., Florida, is rapidly nearing extinction. While censusing the population on St. Johns National Wildlife Refuge on 9 August 1976, we noted an unmated, color-banded male sparrow had abandoned a territory defended since 10 June to feed two recently fledged Red-winged Blackbirds (*Agelaius phoeniceus*) about 50 m away. The mother of the brood was completely tolerant of the sparrow's activity, despite the sparrow's strenuous efforts to keep her away. Both birds fed the young until 12 August. Among 13 food items brought by the sparrow were five grasshoppers and three spiders (cf. Howell, Florida Bird Life, Coward-McCann, New York, New York, 1932). Based on 736 min of observation during these 4 days, foraging accounted for 36% of the sparrow's activity, food delivery for 17%, singing for 18% and aggression toward the female red-wing for 8%; the remaining time was spent on perch or in unknown activity. Mean duration of the red-wing's foraging absences was longer than the sparrow's (8 min vs 14 min, $t = 2.40$, df = 36, $P < 0.05$, N = 22 and 16, respectively), and she spent a greater proportion of her time foraging (75%).

Most instances of interspecific helping have involved adults actively or recently engaged in reproduction (Skutch, Condor 63:198–226, 1961). While the color-banded sparrow was seen with a female and young in 1973 and presumably had ample additional breeding experience, we are convinced, based on 5 months of observation, that he was unmated and had neither nest nor young in 1976. Factors which may have contributed to his abnormal behavior are unclear. Between 1970 and 1976, wildfires reduced the population of Dusky Seaside Sparrows on St. Johns NWR from 110 to 12 (11 ♂♂, 1 ♀). During spring 1976, local variation in the rate of vegetative recovery, coupled with rapid flooding due to heavy rains, resulted in considerable shifting of sparrow territories. Prior to feeding the red-wings the sparrow was occupying his second territory of the year, the first (occupied 4 May–7 June) having been flooded. We believe that the low level of the population, the shortage of females and perhaps the instability of sparrow territories may have acted individually or in concert to prompt this male's unusual behavior.

These data were collected while JLR was conducting research for an M.S. degree at the University of Georgia. Support for this study was provided by the U.S. Fish and Wildlife Service.—James L. Rakestraw, *School of Forest Resources, Univ. Georgia, Athens, Georgia 30602* and James L. Baker, *Merritt Island National Wildlife Refuge, Titusville, Florida 32780.* (Present addresses: JLR: *Museum of Natural History, Univ. Kansas, Lawrence, Kansas 66045* and JLB: *Jacksonville Area Office, U.S. Fish and Wildlife Service, 15 N. Laura St., Jacksonville, Florida 32202.*) *Accepted 24 June 1980.*

Wilson Bull., 93(4), 1981, pp. 541–542

Statistical significance and density-dependent nest predation.—Bradley Gottfried (Wilson Bull. 90:643–646, 1978) recently published a note on an experimental study of the effect of nest density on nest predation. He tested the null hypothesis that there was no difference between the experimental and control, the high and low density plots. The study was well thought out and presented, and is in fact a model for the kind of information that alone will convince us that our hypotheses are or are not valid. Dr. Gottfried's excellent study produced results, however, that did not show a statistically significant difference between the rates of nest predation on artificially placed nests at high densities, and similar nests placed at low densities. This result led him to accept the hypothesis that there was no density-dependent predation in the field he was studying, in contrast to the results reported in other studies. In his discussion he then addressed the question of potential difference between the old field plots he studied and the plots that others have studied. To show that this difference exists, we need to show that his data were significantly different from the data presented by scientists who worked in either marshes or in forests, both of whom have found statistically significant differences in nest predation between habitats with high and low densities of nests.

For example, one of the studies which he supposed produced different results from those in his study is Fretwell's (Populations in a Seasonal Environment, Princeton Univ. Press, Princeton, New Jersey, 1972). Fetwell found that Field Sparrows (*Spizella pusilla*) nesting in two early succession pine forests at two different densities had nesting success rates of 0.21 (high nest density) and 0.33 (low nest density). Fretwell presented this difference as being statistically significant, but a critique by Dow (Wilson Bull. 90:291–295, 1978) on the technique used by Fretwell (1972) is valid and suggests that the difference should be re-evaluated by a more appropriate method. Fretwell, however, did note the same trend in all 3 years that he collected data, and also found a statistically significant trend in an intensive within-habitat study. The difference discovered by Gottfried (1978) for 1 week of nest exposure was 0.69 success in the high density plot and 0.76 success in the low density plot. Since the normal successful nest is exposed for at least 3 weeks, we can estimate the magnitude of this difference for nests that would be comparable to those in Fretwell's study by taking these survival rates to the third power. This assumes that these nests would be replaced as lost, which in fact is what would occur in a natural situation. This yields 0.33 success for the high density plot and 0.45 for the low density plot. Thus, at high densities, sucess was about 27% lower than the value in the low density plots. This compares to the difference of 37% in Fretwell's study.

We attempted to see if this difference in studies was statistically significant, by doing a z-test on the difference between the differences. We first corrected each survival rate for the average in the study in which it was measured, since we are interested in comparing relative and not absolute differences. For example, a difference in survival rates of 10% and 5% is more significant than a difference of 50% and 40%, and Fretwell's nests survived less well than Gottfried's nests. We tested the null hypothesis that the 37% density-dependent effect in Fretwell's study is the same as the 27% density-dependent effect in Gottfried's study using the following formula:

$$Z = \frac{\frac{P_{11}}{\bar{P}_1} - \frac{P_{12}}{\bar{P}_1} - \frac{P_{21}}{\bar{P}_2} + \frac{P_{22}}{\bar{P}_2}}{\sqrt{Pq}\left(\frac{1}{\bar{P}_1^2 n_{11}} + \frac{1}{\bar{P}_1^2 n_{12}} + \frac{1}{\bar{P}_2^2 n_{21}} + \frac{1}{\bar{P}_2^2 n_{22}}\right)}$$

where

P_{11} = proportion of successful nests in Fretwell's low density plot,
P_{12} = proportion of successful nests in Fretwell's high density plot,
P_{21} = proportion of successful nests in Gottfried's low density plot,
P_{22} = proportion of successful nests in Gottfried's high density plot,

$$\bar{P}_1 = \frac{P_{11} + P_{12}}{2}, \quad \bar{P}_2 = \frac{P_{21} + P_{22}}{2}, \quad P = \frac{\bar{P}_1 + \bar{P}_2}{2}, \quad q = 1 - P,$$

n_{11} = sample size in Fretwell's low density plot,
n_{12} = sample size in Fretwell's high density plot,
n_{21} = sample size in Gottfried's low density plot,
n_{22} = sample size in Gottfried's high density plot.

The value obtained is 0.33. If all the ratios in the numerator are normally distributed with variances as calculated beneath the square root bracket in the denominator, then the probability of the value calculated follows a z-distribution, since the sum of normally distributed variates is also normally distributed. These ratios are all calculated from means and should therefore be normally distributed. A z value of 0.33 is not large enough to reject the null hypothesis ($P < 0.37$).

Statistical significance is a statement about sample size, not about a biological phenomenon. The presence of statistical significance in some data simply means that one's sample is sufficiently large to detect the biological differences that are present. Absence of statistical significance means that one's data are insufficient to detect any measurable biological differences that are present. The inability to detect a difference does not justify the conclusion that no differences are present, however. Gottfried's data, which are invaluable and beyond any doubt deserve our attention, are yet too few (one breeding season, 136 nests) for us to know whether or not there is any biologically significant density dependence of nest predation in old fields. They are also too few for us to know whether or not there are any differences between old fields and marshes and successional woodlands.

If Gottfried replicated his study 4.5 times, he would have an 80% chance of detecting the presence of a density effect (Sokal and Rohlf, Biometry, W. H. Freeman and Co., San Francisco, California, 1968:609). To show differences between habitats, we would need many more replications in both woods and old field. Replicating both Gottfried's experiments and Fretwell's studies the same number of times, assuming all samples are the size of Gottfried's and correcting to equalize mean predation rates between old field and woods, it would take over 30 sets of results identical to Fretwell's and Gottfried's (or results showing a greater difference) to demonstrate significance.—Stephen D. Fretwell and Frank S. Shipley, *Div. Biology, Kansas State Univ., Manhattan, Kansas 66506.* *Accepted 18 Nov. 1980.*

Wilson Bull., 93(4), 1981, pp. 542–547

A comparison of nest-site and perch-site vegetation structure for seven species of warblers.—One aspect of the study of avian niche structure has involved habitat relationships of breeding birds. In general, birds seek a characteristic vegetation-structure type, their niche-gestalt (James, Wilson Bull. 83:215–236, 1971), in which to establish a territory (Hilden, Ann. Zool. Fenn. 2:53–75, 1965). This territory provides many breeding passerines with suitable areas for singing, feeding and nesting. Some previous descriptions of avian habitat relationships (James 1971; Whitmore, Wilson Bull. 87:65–74, 1975; Smith, Ecology 58:810–819, 1977) have been based on information collected from within a 0.04-ha circular

Table 1
Bird Species and Number of Circular Plots Used in the Analyses

Species	Habitat[a]	Circles	Number of nests	Perches
Nashville Warbler (*Vermivora ruficapilla*)	edge	13	3	3[b]
Northern Parula (*Parula americana*)	forest	16	4	3
Yellow Warbler (*Dendroica petechia*)	open	14	4	4
Chestnut-sided Warbler (*D. pensylvanica*)	open	16	2	2
Palm Warbler (*D. palmarum*)	edge	4	2	2
Ovenbird (*Seiurus auricapillus*)	forest	18	4	3
Common Yellowthroat (*Geothlypis trichas*)	open	17	4	0
Total		98	23	17

[a] Collins et al. (Oikos, In press), based upon analysis of 211 plots for 16 species of warblers.
[b] Number of perch plots with corresponding nest-site samples.

plot centered on a song perch within the territory of a singing male. Various structural attributes of the vegetation are recorded in these plots (James and Shugart, Audubon Field Notes 24:727–736, 1970), and several circles are sampled to determine the general habitat structure of each species. In the past, these data have been presented as averages and thus do not permit analysis of subtle within-habitat structural differences. The purpose of my research was to determine if differences in vegetation structure occur within the territories of several species of Parulidae (Table 1). This study is part of a larger project analyzing the habitat relationships and geographic habitat variation of the warblers in Maine and Minnesota.

Study area and methods.—This study was conducted in Itasca State Park located in Clearwater, Hubbard and Becker counties, in north-central Minnesota. The park contains 12,500 ha, of which 941 ha (7%) are lakes and ponds (Hansen et al., Univ. Minnesota Agric. Exper. Stat. Bull. 298, 1974). The area is located in the hemlock (*Tsuga*)-white pine (*Pinus strobus*)-northern hardwoods forest region (Braun, Deciduous Forests of Eastern North America, Blakeston Press, Philadelphia, Pennsylvania, 1950). Both logging and fires have created a diversity of vegetation types in the region, ranging from aspen coppice to mature upland spruce (*Picea*)-fir (*Abies*) forests, hardwood stands and pine stands. Parmelee (Loon 49:81–95, 1977) reported 27 species of warblers in the park, of which 13 are considered common nesting species.

Additional habitat data were obtained for Nashville and Palm warblers from the Red Lake Peatlands Natural Area, northern Beltrami Co., Minnesota. The vegetation in this region consists of forested "islands" of small black spruce (*Picea mariana*) and tamarack (*Larix laricina*), dense, low ericacious shrubs and a continuous ground cover of sedges and *Sphagnum* spp.

To determine if within-habitat variability occurs, two 0.04-ha circular plots, one at the nest-site and one at a perch-site, were sampled within the territory of a breeding male bird. Thirteen structural characteristics of the vegetation were measured in each circle (Table 2). Supplemental perch-site data were obtained from another data set in which nest-sites were not located. A total of 23 nest-sites and 75 perch-sites were sampled (Table 1).

Statistical differences between the vegetation structure of the nest-sites and perch-sites were measured by the Wilcoxon matched-pairs signed-ranks test. This test determines the

Table 2

Vegetation Structure Variables Considered in the Analysis of 0.04-ha Nest- and Perch-site Samples[a]

GC	Percent ground cover—no. of sightings of ground cover vegetation at 20 evenly spaced points across a transect dividing the circle
CC	Percent canopy cover—no. of sightings of canopy vegetation at 20 evenly spaced points across a transect dividing the circle
SC	No. of contacts of shrub vegetation by the outstretched arms at 20 evenly spaced points across a transect dividing the circle
CO	Percent coniferous vegetation in the canopy at 20 evenly spaced points across a transect dividing the circle
CH	Canopy height
SPT	No. of species of trees
T1	No. of trees 7.5–15 cm dbh
T2	No. of trees 15.1–23 cm dbh
T3	No. of trees 23.1–30 cm dbh
T4	No. of trees 30.1–38 cm dbh
T5	No. of trees 38.1–53 cm dbh
T6	No. of trees 53.1–68.5 cm dbh
T7	No. of trees greater than 68.5 cm dbh

[a] After James and Shugart (1970).

direction and magnitude of differences (Siegel, Nonparametric Statistics for the Behavioral Sciences, McGraw-Hill, New York, New York, 1956) between the structural characteristics of nest- and perch-sites. Comparisons for each species were made at two levels: (1) individual nests with corresponding perch-sites, and (2) average nest-site structure vs average perch-site structure.

Typically, 0.04-ha-plot data are analyzed by multivariate ordination techniques. These methods elicit habitat patterns and indicate the most important vegetation variables which produce these patterns. In this case, discriminant function analysis (DFA) was applied to each species habitat structure matrix to determine if vegetation structure variables can discriminate between nest- and perch-sites. DFA combines the habitat variables in a stepwise fashion into the linear discriminant function which can best segregate nest-sites from perch-sites. The advantage of the multivariate DFA over the univariate Wilcoxon tests is that the former method incorporates the variability inherent in any habitat structure data set. For a description of DFA see Morrison (Multivariate Statistical Methods, 2nd ed., McGraw-Hill, New York, New York, 1979). The DFA was performed with BMDP (Dixon, Biomedical Computer Programs, Univ. California Press, Los Angeles, California, 1977) on the University of Oklahoma IBM 360/50 computer.

Results and discussion.—The general habitat structure of the seven species of warblers ranged from open-country to forest and forest-edge nesting species (Table 1). In spite of the small sample size, some patterns and differences in nest-site and perch-site structure can be extracted.

Only 29% (5/17) of the nest-sites had vegetation structures that were significantly different from the corresponding perch-sites within a territory (Table 3). Four of the five differences were in open-country nesting species. The differences in the structurally simple open habitats

TABLE 3
COMPARISON OF NEST-SITE VS PERCH-SITE VEGETATION STRUCTURE[a]

Species	Nest-perch comparison	T[b]	*P*	N
Northern Parula	N2-P2	4.0	0.01	11
Yellow Warbler	N1-P1	3.5	0.05	9
Yellow Warbler	N3-P3	0.0	0.05	7
Chestnut-sided Warbler	N1-P1	4.0	0.05	8
Chestnut-sided Warbler	N2-P2	0.0	0.01	9

[a] Based on the Wilcoxon matched-pairs signed-ranks test (Siegel 1956); 5 of 17 comparisons were significantly different.
[b] T = sum of ranks, *P* = probability level, N = number of variables in comparison.

of the Yellow and Chestnut-sided warblers were due to the greater number of trees at perch-sites which increased canopy cover, tree height and percent conifer in the canopy. The perch-site of the Northern Parula had higher ground and shrub cover, and percent conifer in the canopy than at the nest location.

If the nest-site and perch-site data for each species are averaged and again compared by the Wilcoxon test, the within-territory structure of the Northern Parula is no longer statistically different (N = 12, T = 21). However, both the Yellow and Chestnut-sided warblers still showed significant differences (N = 12; T = 1 and T = 9, respectively). Average perch-site variables of these species again contained greater tree component structure than average nest-sites corroborating the results of the within-territory comparisons.

The F-values for the six discriminant functions were significant for only two species—Common Yellowthroat and Northern Parula (Table 4). Percent conifer and canopy height significantly separate Common Yellowthroat nest- and perch-sites. However, the DFA reclassified one perch-site as a nest-site, and vice versa. Thus, within this data set, some structural overlap occurs between the two types of sites.

Eight variables entered into the Northern Parula discriminant function, most of which were tree size-class variables. The nests of this species were located in forest to forest-edge habitat

TABLE 4
DISCRIMINANT FUNCTION ANALYSIS OF SPECIES NEST-SITE VS PERCH-SITE STRUCTURE

Species	Variables entered[a]	F-value (df)	*P*	Number reclassified
Nashville Warbler	T2, CO	3.49 (2, 10)	0.10	1
Northern Parula	T3, T2, T6, CH, T5, SPT, GC, T4	5.69 (8, 7)	0.02	0
Yellow Warbler	CH, SPT, SC, T1	1.79 (4, 9)	NS	2
Chestnut-sided Warbler	CC	3.83 (1, 14)	0.10	2
Ovenbird	T3, T5	2.36 (2, 15)	NS	5
Common Yellowthroat	CO, CH	4.50 (2, 14)	0.05	2

[a] Variables are listed in order of entry into the discriminant function; see Table 2 for definition of variables.

with variable numbers of large deciduous and coniferous trees, and a relatively open canopy. Perch-sites were also variable yet they were most often located in the forest rather than at the forest edge. No nest- or perch-sites were reclassified, so complete discrimination between these sites is possible.

In summary, it appears that for the ground nesting Palm Warblers, Nashville Warblers and Ovenbirds, minimal differences exist between nest-site and perch-site structure. The Yellow and Chestnut-sided warblers showed significant differences in individual and average nest-site/perch-site comparisons, yet these nonconformities did not appear in the DFA. The Common Yellowthroat showed a difference only in the multivariate analysis. Lastly, both uni- and multivariate comparisons of the Northern Parula nest- and perch-site variables imply locally different within-habitat vegetation structure.

Several factors may cause the differences observed in these tests, one of which is the inherent variability of the vegetation. Curtis (The Vegetation of Wisconsin, Univ. Wisconsin Press, Madison, Wisconsin, 1959) stressed the compositional variation of vegetation and concluded that the same plant communities in a region resemble each other only to the extent of 50–70%. Many territories of forest nesting species are greater than 0.5 ha (Bent, Life Histories of North American Wood Warblers, U.S. Natl. Mus. Bull. 203, 1953) thus incorporating the natural variability of the vegetation. Secondly, the male selects and defends the territory, whereas the female chooses the nest-site. Different criteria are selected at each site: conspicuousness for male displays vs sheltered nest location. Thirdly, previous ecological studies of warblers have shown that males and females use different parts of the territory (Morse, Ecology 49:779–784, 1968; Ecology 54:346–355, 1973; Busby and Sealy, Can. J. Zool. 57:1670–1681, 1979). In particular, males foraged farther from the nest and higher in the canopy than did females. Finally, the selection of a perch-site as the center of a circular plot implies some degree of vegetation structure. Therefore, the wide ranging foraging behavior of males, large territories and differential territory use combine to introduce within-habitat variability.

Many stimuli, such as specific aspects of habitat structure, presence of other birds, food and previous breeding success, are proximate factors which can combine to elicit a territorial settling response in breeding birds (Hilden 1965). The measurement of vegetation structure is a reliable means of summarizing these stimuli since the physical habitat provides the background for the variables in the life cycle of a breeding bird. The suitability of the 0.04-ha-circle technique for summarizing and describing the 3-dimensional habitat structure of a species remains valid. Certain caveats, however, should be considered. James (1971) stated that centering a circular plot on a song perch "may give a biased view of habitat for species which occur in open areas and choose singing perches in places different from their foraging areas, but this objection is minimized in the forest." She later reiterated this statement noting that the 0.04-ha-circle method was only suitable for areas with trees (James, Am. Birds 32:18–21, 1978). However, my evidence for the Northern Parula suggests that within-habitat variability exists in forest nesting species. The technique is still very useful for describing the habitat of breeding birds, but locating circular samples around nest-sites or around female foraging areas is recommended whenever possible to incorporate within-habitat variation. Otherwise, caution should be used when interpreting habitat structure since perch-sites of forest and open-country nesting species may overestimate the tree component of the habitat.

Acknowledgments.—I would like to thank the Behavioral Ecology class and the Field Ornithology class for providing some nest locations. I especially thank my wife, Pat, for field assistance. Dwight Adams, Karen Dooley, David Gibson, Frances James, Paul Risser and Gary Schnell provided comments on earlier drafts of the manuscript. This research was supported by a grant from the Chapman Memorial Fund and by a Malvin and Josephine Herz

Foundation Summer Fellowship to the University of Minnesota Biological Station.—Scott L. Collins, *Dept. Botany and Microbiology, Univ. Oklahoma, Norman, Oklahoma 73019. Accepted 8 Nov. 1980.*

Wilson Bull., 93(4), 1981, pp. 547–548

Use of artificial perches on burned and unburned tallgrass prairie.—Kendeigh (Condor 43:165–175, 1941) stated that territorial male birds may lack sufficient perches in grasslands from which to conduct display activities. I investigated the importance of artificial perch availability to tallgrass prairie birds, from 7 June–31 July 1979, at the Konza Prairie Research Natural Area. This area of native bluestem (*Andropogon*) prairie is located in the extreme south-central portion of Riley and northern portion of Geary counties, Kansas.

Two areas on annually burned prairie and two on unburned prairie were selected for study. Artificial perches were added to one annually burned prairie (35 ha) and one unburned prairie (25 ha) with the other annually burned prairie (12 ha) and unburned prairie (39 ha) used as controls. The experimental sites were located adjacent to each other. Control sites were separated from experimental sites and from each other.

Perches were 2 × 2 cm wooden stakes, 1.5 and 2.0 m above ground level. Twenty-three perches were placed on the 35-ha annually burned prairie and 17 perches on the 25-ha unburned prairie, giving approximately equal perch density (0.67 perch/ha) in each area. The perches were placed in 15 m^2 subplots in each experimental area using randomly generated numbers. Use of perches in burned and unburned prairie and perch height preference were recorded during 36 spot check censuses. Spot check censuses were performed by approaching each perch within 100 m and noting the species and activity of each bird.

A vegetation density analysis on each plot was made using randomly selected 5 m^2 areas, for which standing height and percent cover by life form were recorded. For each area, 50% of the total area was analyzed.

Vegetation analyses indicated that the following plants were dominant. Grasses included: big bluestem (*Andropogon gerardi*), little bluestem (*A. scoparius*), windmillgrass (*Chloris verticillata*), switchgrass (*Panicum virgatum*) and side-oats grama (*Bouteloua curtipendula*). Dominant forbes were lead plant (*Amorpha canescens*), prairie wild indigo (*Baptisia leucophaea*), Baldwin ironweed (*Vernonia baldwini*), wild alfalfa (*Medicago lupulina*), fingeleaf ruellia (*Ruellia humilis*), tick-trefoil (*Desmodium illinoense*), butterfly milkweed (*Asclepias tubersoa*) and narrow-leaved milkweed (*A. stenophylla*). Woody vegetation consisted of the prairie rose (*Rosa arkansana*) and buckbrush (*Symphoricarpos abiculatus*). The mean standing height of vegetation for burned and unburned prairie was 27.66 cm and 45.50 cm, respectively.

Eleven of 23 perches (48%) were used on the burned area and 5 of 17 perches (29%) on the unburned area. This difference was not significant using the Chi-square test for equal proportions ($\chi^2 = 1.18$, df = 1, $P = 0.17$). Lack of significance may have been caused by small sample size and similarity in proportions of bird density/perch use in each area.

Species observed using perches in the burned area, in order of decreasing perch use were Dickcissel (*Spiza americana*), Eastern Meadowlark (*Sturnella magna*), Red-winged Blackbird (*Agelaius phoeniceus*), Brown-headed Cowbird (*Molothrus ater*), Common Nighthawk (*Chordeiles minor*), Grasshopper Sparrow (*Ammondramus savannarum*), Eastern Kingbird (*Tyrannus tyrannus*) and Upland Sandpiper (*Bartramia longicauda*). The following birds were found to use perches in the unburned area in order of decreasing perch use: Eastern Meadowlark, Grasshopper Sparrow, Dickcissel and Brown-headed Cowbird. Birds using

perches engaged in territorial song, establishment of territorial boundaries, call notes, preening and resting. Birds seemed to prefer natural perches to artificial perches.

No difference in average male density between areas with and without perches in unburned prairie (31 ♂♂/ha in both) was observed. In the burned prairie, however, area without perches had a density twice as great as the area with perches (56 ♂♂/ha vs 27 ♂♂/ha). This difference was believed to be due to large numbers of Dickcissels and Red-winged Blackbirds attracted to a stream in the area. When the data with all birds were tested, differences in density between the two areas were significant (Wilcoxon signed ranks test, $P = 0.008$); however, when Dickcissels and Red-winged Blackbirds were deleted from the analyses, the difference was not significant ($P = 0.11$) indicating that these two species had measurable impacts on the observed densities.

This research was funded by the National Science Foundation's Undergraduate Research Participation Program at Kansas State University. Thanks are due to John L. Zimmerman (Biol. Dept., KSU), Elmer Finck (Biol. Dept., KSU) and VPI & SU Statistical Consulting Laboratory.—JANET JEAN KNODEL-MONTZ, *Fisheries and Wildlife Dept., Virginia Polytechnic Inst. and State Univ., Blacksburg, Virginia 24061.* *Accepted 15 Aug. 1980.*

Wilson Bull., 93(4), 1981, p. 548

Juvenile Peregrine Falcon swoops on Roseate Spoonbills.—On 26 September 1979, I observed an immature Peregrine Falcon (*Falco peregrinus*) swoop down on two Roseate Spoonbills (*Ajaia ajaja*) which were foraging about a meter apart in an impoundment on the Merritt Island National Wildlife Refuge, Brevard Co., Florida. My watch began at the impoundment at 08:00, and the falcon was noted in a dead white mangrove (*Laguncularia racemosa*) at 09:20. At 10:04 the falcon left the tree and headed directly toward the spoonbills, which were 20 m away, in a gliding-flapping flight. As the falcon approached the spoonbills, they stopped feeding, stood erect, faced the falcon and flashed their wings. The wing flash consisted of opening the wings to the wrist and allowing the remainder of the wing to droop with the primaries near the body. After the wing flashes, the falcon turned abruptly and landed in a nearby mangrove tree. Approximately 10 min later, the foraging spoonbills were 10 m apart when the falcon swooped down on one bird. The reaction of the spoonbill was the same. Although both spoonbills continued to feed for an additional 10 min before departing, they continuously watched the falcon which remained in the area for about an hour.

The Roseate Spoonbill is a relatively large bird to be taken by a Peregrine Falcon, and this episode may have been a "mock attack" or play. However, it is possible the swoops were an attempt by the falcon to flush the spoonbills so it could take one. George (Raptor Res. 13:88–90, 1979) observed an immature Peregrine Falcon strike a Snow Goose (*Chen caerulescens*) and Cade (Univ. Calif. Publ. Zool. 63:151–267, 1961) found a Peregrine could take a 1400 g Black Brant (*Branta bernicla*) and a 1300 g Canvasback (*Aythya valisineria*). Palmer (Handbook of North American Birds, Vol. 1, Yale Univ. Press, New Haven, Connecticut, 1962) states the Roseate Spoonbill weighs up to 1600 g, and one immature bird weighed 1169 g. Because no other flight intention movement was observed, and the posture of the spoonbills was different from a high intensity threat display (body axis parallel to the ground, wings held above the body and neck outstretched [pers. obs.]), it is possible the wing flashes gave the falcon information on the size of the birds or may have served to increase their effective size. Cade (1961) observed a similar behavior in a molting Canada Goose to ward off a Peregrine Falcon.

I thank Peter Wrege for comments on this note.—E. SCOTT CLARK, *Merritt Island National Wildlife Refuge, Titusville, Florida 32780.* (Present address: *LMNPD-RE, US Army Corps of Engeneers, P.O. Box 60267, New Orleans, Louisiana 70160.*) *Accepted 29 Aug. 1980.*

Wilson Bull., 93(4), 1981, p. 549

Symbiotic interaction between Starlings and deer.—The symbiotic relationship between oxpeckers (*Buphagus* spp.) and large African mammals is well documented (Rice, Auk 80:196–197, 1963). A few North American birds have been observed eating ectoparasites on large mammals. Most of these associations involve ungulates and corvids (Dixon, Condor 46:204, 1944; Rice and Mockford, Wilson Bull. 66:272–273, 1954). A recent note describes interactions between Scrub Jays (*Aphelocoma coerulescens*) and feral hogs (*Sus scrofa*) (Baber and Morris, Auk 97:202, 1980). I observed two similar interactions between Starlings (*Sturnus vulgaris*) and white-tailed deer (*Odocoileus virginianus*) in central Wisconsin where Starlings commonly feed on insects flushed by grazing cattle. Observations were made with a 15 × 60 spotting scope.

On 8 July 1979, at 20:50 CST, I saw an adult female deer walking through a grass-shrub area; an adult Starling was perched on her nose. The bird moved up to the crown of the deer's head, down the neck and back and returned to the head, ostensibly probing for ectoparasites; the deer showed no reaction. The observation lasted 10 min while the deer moved over 200 m and then out of view.

On 16 July 1979, at 09:15 CST, I saw an adult Starling on the head of an adult deer of unknown sex. The deer was on a little-used road which bisected a pastured area interspersed with oak (*Quercus* spp.) woodlots. The deer was visible for only 15 sec before it disappeared into cover and was apparently oblivious to the presence of the Starling. Riney (Condor 53:178–185, 1957) noted similar complacency in Scrub Jay-mule deer (*O. hemionus*) interactions. That advanced feeding behavior is extensive in another sturnid, the oxpecker, suggests that family-related learning traits may be developing within local Starling social groups as Baber and Morris (1980) speculated for Florida Scrub Jays.

I wish to thank Raymond K. Anderson for helpful comments on this manuscript.—Robert K. Murphy, *College of Natural Resources, Univ. Wisconsin at Stevens Point, Stevens Point, Wisconsin 54481.* *Accepted 10 Oct. 1980.*

Wilson Bull., 93(4), 1981, pp. 549–550

Cattle Egrets feeding in association with human workers.—The foraging strategy of Cattle Egrets (*Bubulcus ibis*) in attendance of grazing cattle is well-known. Their association of a commensalistic nature, with domestic and wild ungulates is well-documented (Heatwole, Anim. Behav. 13:79–83, 1965; Ali and Ripley, Handbook of Birds of India and Pakistan, Vol. 1, 1968; Jenni, Ecol. Monogr. 39:245–270, 1969). Cattle Egrets also use human activity to their advantage in so far as following plows, tractors, vehicles, etc. for the purpose of feeding. However, to the best of my knowledge, there are no reports of Cattle Egrets associating with human beings on foot, for food procurement in the field. The present note is a report on such findings.

During the past few years of bird watching, I often visited a large farmland area, part of which is swampy, spanning about 300 ha along the Dabhoi Road, approximately 10 km from Baroda (73°13′E, 22°18′N), Gujrat State, India. This farmland, irrigated with sewage water from the sewage treatment plant of Baroda City Corporation, is the favorite haunt of a large number of migratory and resident birds, including a large population of Cattle Egrets. Much of the area is covered with native grasses harvested for use as cattle fodder. Many laborers make a living nearly year-round manually cutting grass with sickles. Small groups of egrets associate with the laborers, capturing insects flushed during harvesting operations.

On commencement of harvesting, the egrets walk right up to the laborers with apparent confidence. As the workers advance in the field, the egrets also keep pace, remaining within 0.5–1 m of the humans. However, the egrets have not been observed picking insects off the laborers' legs, as they commonly do with cattle. At times, Pond Herons (*Ardeola greyii*) also feed with the Cattle Egrets in a similar manner. It has yet to be ascertained whether the egrets are following humans preferentially. Many egrets are seen feeding by themselves in the field and along the flowing water channels. Small groups of egrets also follow the few water buffalo (*Bubalus bubalis*) grazing at this locality.

The commensal feeding of *A. greyii* with the Cattle Egrets using human workers as 'beaters' is noteworthy. Instances of Squacco Herons (*A. ralloides*) feeding gregariously among cattle, as do Cattle Egrets, are known (Cramp and Simmons, The Birds of the Western Palearctic, Vol. 1, 1977). Furthermore, the behavior of *A. greyii* and *A. ralloides* is considered to be quite similar (Cramp and Simmons 1977). There is considerable discussion as to the taxonomic relationship of the Cattle Egret, and Payne and Risley (Misc. Bull. Mus. Zool., Univ. Michigan, No. 150, 1976) concluded that *B. ibis* is not closely related to *A. greyii*. Thus, additional information on commensalistic feeding behavior of species of *Ardeola* could facilitate further understanding of the taxonomic relations of these herons.

The critical comments on the note and highly useful suggestions from J. Kushlan and D. Mock are gratefully acknowledged.—G. K. Menon, *Dept. Zool., M. S. Univ., Baroda, India. Accepted 10 Sept. 1980.*

Wilson Bull., 93(4), 1981, pp. 550–551

Scrub Jay captures Hermit Thrush in flight.—The opportunism demonstrated by many corvids in obtaining food has been well documented (Bent, U.S. Natl. Mus. Bull. 191, 1946; Goodwin, Crows of the World, Comstock/Cornell Univ. Press, Ithaca, New York, 1976; Coombs, The Crows: a study of the corvids of Europe, B. T. Batsford Ltd., London, England, 1978). Predatory behavior by corvids is not unusual, but prey rarely includes birds in flight. Use of the feet to seize flying birds has been reported for several species of *Corvus* (see Coombs 1978 for review; Heathcote, Br. Birds 71:134–135, 1978) and at least once for jays (Carothers et al., Wilson Bull. 84:204, 1972). A Magpie (*Pica pica*) presumably used its wings to "beat" a Swift (*Apus apus*) to the ground (Pulman, Br. Birds 71:363, 1978). Our report concerns a Scrub Jay (*Aphelocoma coerulescens*) which used its bill to capture a Hermit Thrush (*Hylocichla guttata*) in flight.

The incident occurred at 12:30 on 28 September 1979 on the campus of the University of California at Davis. A Hermit Thrush flew from beneath a hedge to a sunlit area where flying insects were visible. The bird hovered, apparently attempting to capture the insects. Seconds later, a Scrub Jay flew from the same hedge and attacked the hovering thrush. After a few seconds of struggling and a short pursuit, the jay managed to grasp the thrush by the neck. Still flying, the jay carried the thrush in its bill to a branch in a nearby tree. The jay placed its foot on the thrush, released the bird's neck and struck the thrush's head with two rapid strokes of its bill. The thrush, which had been screaming distress calls since its capture, fluttered briefly and became silent. The jay then began plucking feathers from the thrush's back.

In order to examine the dead thrush, we frightened the jay from its prey. The Hermit Thrush had a single hole in the right side of its head, just behind the eye. Hemorrhaging was evident on the right side of the neck. Remiges of the left wing and contour feathers of the back and neck had been removed, but no flesh had been torn. Internal examination

revealed that the thrush was an immature female. Insect remains, almost exclusively elytra of unidentified beetles, were present in the gizzard.

Past sightings of jays killing birds capable of flight did not involve prey as large as the Hermit Thrush. Blue Jays (*Cyanocitta cristata*) killed a Purple Finch (*Carpodacus purpureus*) (Downs, Bird-Banding 29:244, 1958), a Yellow-rumped Warbler (*Dendroica coronata*) (Johnson and Johnson, Wilson Bull. 88:509, 1976) and a House Sparrow (*Passer domesticus*) (Master, Wilson Bull. 91:470, 1979); a Mexican Jay (*A. ultramarina*) caught an unidentified sparrow (Roth, Condor 73:113, 1971); and Steller's Jays (*C. stelleri*) killed Gray-headed Juncos (*Junco caniceps*) and a Pygmy Nuthatch (*Sitta pygmaea*) (Carothers et al. 1972). Only the Pygmy Nuthatch was flying when captured. The Scrub Jay's method of holding food items with its feet when perched was typical of corvids (Bent 1946, Goodwin 1976), as was killing a vertebrate by striking repeated blows to the prey's head near the eye (Bent 1946; MacCracken, Auk 66:210, 1949; Bateman and Balda, Auk 90:39–61, 1973; Maser, Wilson Bull. 87:552, 1975; Mulder et al., Condor 80:449–451, 1978).

We thank D. W. Anderson, C. Ely, B. J. Gray and D. G. Raveling for comments on the manuscript.—M. Robert McLandress, *Div. Wildlife and Fisheries Biology, Univ. California at Davis, Davis, California 95616* and Ilse McLandress, *RIM Ecology Ltd., 203–225 Vaughan St., Winnipeg, Manitoba R3C 1T7 Canada.* *Accepted 10 Sept. 1980.*

Wilson Bull., 93(4), 1981, pp. 551–554

Food habits of Black-bellied Whistling Ducks occupying rice culture habitats.—Apart from a few anecdotal reports (Bent, Life Histories of North American Wildlife, U.S. Natl. Mus. Bull. 130, 1925; Cleare, Birds, The Argosy Co., Georgetown, Guyana, 1938; Haverschmidt, Field Notes on the Black-bellied Tree Duck in Dutch Guyana, Wilson Bull. 59:209, 1947; Giglioli, Crop Histories and Field Investigations, 1951–1957, Br. Guiana Rice Development Co., Georgetown, Guyana, 1959; Haverschmidt, Birds of Surinam, Livingston Publishing Co., Wynnewood, Pennsylvania, 1968) and two studies in southern Texas (Bolen and Forsyth, Foods of the Black-bellied Tree Duck in south Texas, Wilson Bull. 79:43–49, 1967; Bolen and Beecham, Notes on the foods of juvenile Black-bellied Tree Ducks, Wilson Bull. 82:325–326, 1970), the food habits of Black-bellied Whistling Ducks (*Dendrocygna autumnalis*) have been little studied. In 1973, I initiated an ecological study of Black-bellied Whistling Ducks to evaluate the magnitude of their foraging activity in ricefields. Preliminary results (Bourne and Osborne, Black-bellied Whistling Duck utilization of a rice culture habitat, Intercencia 3:152–159, 1978) indicate that overall depredation levels are low even though the ducks ingest newly sown, pregerminated paddy or seed rice (*Oryza sativa*). The purpose of this paper is to present data on the food habits of Black-bellied Whistling Ducks in Guyana, South America, when they occupied rice culture habitats during crop sowing in June 1973 and July–August 1974.

Materials and methods.—I conducted fieldwork in Burma (6°28′N, 57°45′W) at the Mahaicony and Abary Rice Development Scheme (MARDS). Detailed descriptions of the study area and its flora and fauna are available in Giglioli (1959) and Osborne and Bourne (Breeding behavior and food habits of the Wattled Jacana, Condor 79:98–105, 1977). In 1973, two methods were used for obtaining specimens: 15 ducks were shot between 05:00 and 07:16 with the aid of playback vocalizations and 15 were mist-netted between 20:00 and 20:55. Adults and juveniles collected in 1974 were shot between 05:00 and 07:16 with the aid of playback vocalizations. Two ducklings were hand caught in a fallow field on 8 August 1974, at 08:10 and 08:25. Specimens were dissected within 30 min and the entire

alimentary tract of each duck was placed in a separate large-mouth bottle containing 10% formalin. The contents of the esophagus, proventriculus and ventriculus were identified to the lowest taxon possible, and their volumes were determined by water displacement.

Results 1973.—Food items identified from 30 adult Black-bellied Whistling Ducks (15 males, 15 females) indicate that plant material accounted for 97% of the food consumed (Table 1). Most (86%) of this plant food consisted of pregerminated paddy. Other plant foods accounted for 11% of the ducks' diet while animal foods made up only 3% of the birds' fare (Table 1). Most of the animals consumed were invertebrates; the majority were aquatic insects and snails (Table 1). Two ducks (7%) consumed young tadpoles of the marine toad (*Bufo marinus*). Of the 30 ducks examined for their food preferences, 63% ingested animal foods; 37% of these were males and 63% were females.

1974.—Plant foods accounted for 90% of the adults' and juveniles' diets (Table 1). Paddy dominated the adults' diet, constituting 74%, but was less important in the juveniles' diet, accounting for 15% of their food (Table 1). In 1974, adults consumed the same genera and species as the adults did in 1973 (Table 1), but juveniles had eaten the seeds of a grass, *Paspalum* sp., which accounted for 71% of their diet and occurred in 95% of the juveniles sampled (Table 1). Young apple snails (*Pomacea* sp.) were the most important animal foods consumed by juveniles as they accounted for 8.5% of their diet, and occurred in 70% of the sample (Table 1).

Two ducklings analyzed for their food preferences consumed 54% animal foods and 46% plant foods. The plant foods consisted of the seeds of a millet, *Echinochloa* sp. and *Paspalum* sp.; they accounted for 31% and 15% of the diet, respectively. Shorefly (*Scatella stagnalis*) larvae and pupae were found in trace amounts, but the bulk of the animal food consisted of unidentified terrestrial spiders.

Discussion.—Black-bellied Whistling Ducks, like other dendrocygnids, are basically herbivorous (Johnsgard, Waterfowl of North America, Indiana Univ. Press, Bloomington, Indiana, 1975). But at sowing time, cultivated cereals dominate the plant food preferences in Black-bellied Whistling Ducks' diets. For example, corn (*Zea mays*) was the most important constituent in the species' diet in Mexico (Bent 1925), and *Sorgum vulgare* constituted 48% of the species' diet in south Texas (Bolen and Forsyth 1967). Paddy accounted for 86% and 74% of the adult Black-bellied Whistling Duck's diet in Guyana during the early rice growing season. Observations suggest that paddy would become less important in the duck's diet as the growing season progressed because fewer suitable water-planted ricefields would be available as foraging sites. This may explain why paddy accounted for only 15% of the juveniles' diet, since they were collected after the adults were from 22 July–9 August 1974, when planting was almost completed.

Animal foods do not appear to be important in adult and juvenile Black-bellied Whistling Ducks' diets. Even though adults were in breeding condition (as evidenced by gonadal measurements, males, N = 18; left testes mean 24 × 12 mm [10 × 5–32 × 16 mm]; females, N = 17, largest follicle mean 40 mm [3–56 mm]), they only consumed 3% animal food in 1973 and 10% in 1974, while juveniles also ingested 10% animal food in 1974. However, these data could be biased downwards due to the faster digestion of soft-bodied invertebrates in the proventriculus and ventriculus. Ducklings consumed 54% animal foods in this study, suggesting that younger whistling ducks need the higher protein content found in animal foods for growth and development.

Acknowledgments.—Financial support of this investigation was provided by the Frank M. Chapman Memorial Fund, the Rob and Bessie Welder Wildlife Foundation, and Mr. Frederick N. Stevens. I thank the following for contributing ideas and criticisms: David R. Osborne, W. Hardy Eshbaugh, Gary W. Barrett, Michael P. Farrell and Fay M. Edwards. I am particularly indebted to Charles P. Kennard, George Hughes and their staffs of the Guyana Rice Board for providing facilities at MARDS. Finally, I am thankful to Dick L.

Table 1

Volume, Percent and Frequency of Food Items in the Diet of 30 Adult (8–19 June 1973), 5 Adult (16–17 July 1974) and 20 Juvenile (22 July–9 August 1974) Black-bellied Whistling Ducks at Burma, Guyana

	30 Adults 1973					5 Adults 1974					20 Juveniles 1974				
	Volume		Occurrence			Volume		Occurrence			Volume		Occurrence		
Food	ml	%	male	female	%	ml	%	male	female	%	ml	%	male	female	%
Plant															
Cyperus rotundus (tuber)	0.5	0.1	1	0	3.3	1.0	1.3	0	1	20	2.5	0.8	3	1	20
Scleria pterota (seeds)	17.0	4.6	1	4	16.7	7.5	9.9	2	0	40	0.5	0.2	0	1	5
Echinochloa spp. (seeds)	22.5	6.1	2	5	23.3	3.5	4.6	0	1	20	6.0	2.0	3	3	30
Oryza sativa (seeds)	319.0	86.4	15	15	100.0	56.5	74.3	3	2	100	46.5	15.2	10	8	90
Paspalum sp. (seeds											218.0	71.4	11	9	95
Total plant	359.0	97.2	—	—	—	68.5	90.1	—	—	—	273.5	89.6	—	—	—
Animal															
Diptera															
Scatella stagnalis (larve and pupa)	t*	—	2	5	23.3	0.5	0.7	0	1	20	3.5	1.1	2	4	30
Coleoptera															
Calandra sp. (adult)	0.5	0.1	1	0	3.3	1.5	2.0	0	1	20	2.5	0.8	1	0	5
Hydrophilus triangularis (larva)	1.5	0.4	0	2	6.7	1.5	2.0	1	0	20	—	—	—	—	—
Mollusca															
Pomacea sp. (young)	7.0	1.9	4	3	23.3	2.5	3.3	1	1	40	26.0	8.5	8	6	70
Amphibia															
Bufo marinus (larva)	1.0	0.3	0	2	6.7	1.5	2.0	1	0	20	—	—	—	—	—
Total animal	10.0	2.7	—	—	—	7.5	10.0	—	—	—	32.0	10.4	—	—	—

* Trace.

Deonier for identifying insects, to my wife Carol, Patrick Dougal and the Green brothers for assistance in the field. Data are taken from a M.Sc. thesis submitted to Miami University. This is Welder Contribution 195.—Godfrey R. Bourne, *Institute of Environmental Sciences, Miami Univ., Oxford, Ohio 45056.* (Present address: *School of Natural Resources, Univ. Michigan, Ann Arbor, Michigan 48109.*) *Accepted 3 Nov. 1980.*

Wilson Bull., 93(4), 1981, p. 554

House Sparrows flushing prey from trees and shrubs.—House Sparrows (*Passer domesticus*) exhibit much foraging adaptability (Potter, Condor 33:30, 1931; Bent, Life Histories of North American blackbirds, orioles, tanagers, and allies, U.S. Natl. Mus. Bull. 211, 1958; Summers-Smith, The House Sparrow, Collins, London, England, 1963; Marti, Wilson Bull. 85:483, 1973). Guillory at Eunice, St. Landry Parish, Louisiana, on 22 August 1976, and Deshotels at Kaplan, Vermilion Parish, on 13 September 1977, each observed a House Sparrow displaying previously unreported foraging behaviors.

In Eunice, a female was seen searching in a loose 30 × 46 cm cluster of dry southern red oak (*Quercus falcata*) twigs and leaves located on peripheral branches approximately 6 m above ground. The bird shook the leaf cluster by momentarily grasping a twig with her feet and vigorously flapping her wings. The bird repeated this while hopping from twig to twig in the cluster. The bird flushed an unidentified white moth (Lepidoptera) (2.5 cm), captured it in flight and fed it to one of her nestlings. She returned to the same cluster and twice repeated the above actions, catching two more white moths of similar size and fed them to her nestlings. The bird returned to the cluster, probed among the leaves and caught a brown moth (2.5 cm).

In Kaplan, a male House Sparrow was seen flushing beetles (Coleoptera) and white moths from a densely vegetated, flat-topped hedgerow ca. 30 cm high. Prey were flushed from the top of the hedgerow by hopping and wing flapping similar to that of the aforementioned female. The bird stopped occasionally and probed among the leaves and branches, presumably for insects. The bird hovered near moving insects, apparently attempting to flush them. Prey leaving the shrubbery was captured in flight or on a nearby sidewalk, crushed on the concrete, and then consumed.

These behaviors are further examples of opportunistic foraging by House Sparrows.

We wish to thank Dwight J. LeBlanc for his helpful criticisms of the manuscript.—Harland D. Guillory, *Div. Sciences, Louisiana State Univ. at Eunice, Eunice, Louisiana 70535* and Jack H. Deshotels, *Lot 4, Azalia Drive, Youngsville, Louisiana 70592.* *Accepted 6 Oct. 1980.*

Wilson Bull., 93(4), 1981, pp. 554–556

Differential predation by two species of piscivorous birds.—The piscivorous Double-crested Cormorant (*Phalacrocorax auritus*) and White Pelican (*Pelecanus erythrorhynchos*) use distinctly different foraging techniques (Palmer, Handbook of North American Birds, Vol. 1, Yale Univ. Press, New Haven, Connecticut, 1962). Cormorants dive to depths of 20 m and pursue fish. Pelicans scoop fish "dip-net fashion" in water to depths of 1 m.

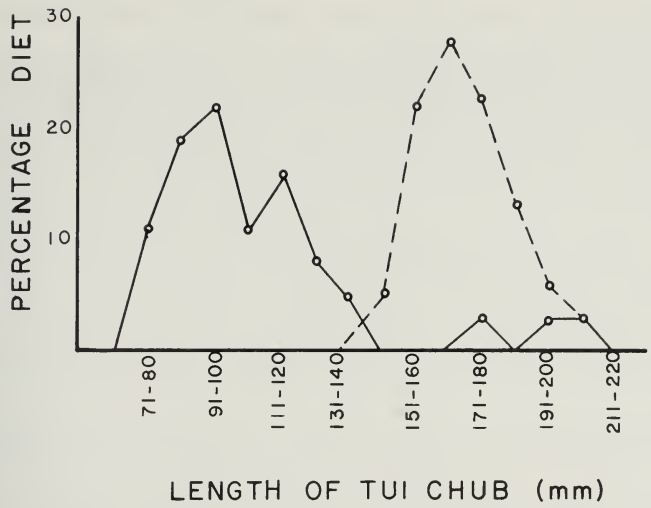


FIG. 1. Percentages of tui chubs of different standard lengths observed in the diets of White Pelicans (solid line) and Double-crested Cormorants (dashed line) at Pyramid Lake, Nevada.

Despite these differences, the species often have similar diets where sympatric (Behle, The Bird Life of Great Salt Lake, Univ. Utah Press, Salt Lake City, Utah, 1958). Such dietary overlap is pronounced at Pyramid Lake, Nevada, where the birds feed heavily upon an indigenous population of tui chub (*Gila bicolor*) which spawns in shallow (<1 m) water from about 1 June–15 August (Kucera, Great Basin Nat. 38:203–207, 1978), during the nestling and pre-fledging phases of cormorant and pelican chick development (Hall, Condor 27:127–160, 1925; Hall, Condor 28:87–91, 1926). Cormorants feed at the lake throughout this period, whereas pelicans forage there only during June (Knopf and Kennedy, Western Birds 11:175–180, 1980). In this study we assessed characteristics of *G. bicolor* preyed upon by the two bird species at Pyramid Lake.

Chicks of cormorants and pelicans readily regurgitate fish if disturbed shortly after they are fed. We collected fish regurgitated in this manner at nesting sites on Anaho Island National Wildlife Refuge, Washoe Co., Nevada on 30 June 1976, within 30 min after chicks were fed. We weighed and measured the fish within 1 h of collection.

We collected 94 *G. bicolor*, totalling 10,625 g, regurgitated by cormorant chicks and 236 fish, totalling 8681 g, regurgitated by pelican chicks. Sixty-four and 37 of these fish, respectively, were intact and could be measured (Fig. 1). The distance from the snout to end of the vertebral column (standard length) of *G. bicolor* regurgitated by cormorant chicks averaged 171.6 mm (SD ± 14.3 mm) while that of fish from pelican chicks averaged 110.1 mm (SD ± 29.7 mm). This difference is statistically significant (t adjusted = 9.22, $P < 0.001$). The variance in length of *G. bicolor* collected from cormorants and pelicans was tested (Lewontin, Syst. Zool. 15:141–143, 1966) and also found to be significantly different ($F = 10.47$, $P <$

0.001). Since the mean standard length of fish regurgitated by cormorants is greater than that of pelicans, this test is conservative.

All fish collected from cormorant chicks were *G. bicolor.* In contrast, of the 344 fish collected from pelican chicks, *G. bicolor* comprised only 39.5% (by weight). Carp (*Cyprinus carpio*) was the predominant fish in the pelican diet (58.6% by weight). White crappie (*Pomoxis annularis*), Tahoe sucker (*Catostomus tahoensis*), Sacramento perch (*Archoplites interruptus*) and brown bullhead (*Ictalurus nebulosus*) comprised only 1.9% of the diet by weight. Carp, plus the other fishes in the pelican diet, are rare or do not occur in Pyramid Lake, and these species were captured by pelicans foraging in outlying wetlands.

Prey size (Storer, Auk 83:423–436, 1966; Ashmole, Syst. Zool. 17:292–304, 1968) and variation in prey size (MacArthur, Geographical Ecology, Harper and Row, New York, New York, 1972; Reynolds, Foods and habitat partitioning in two groups of coexisting *Accipiter*, Ph.D. diss., Oregon State Univ., Corvallis, Oregon, 1979) tend to increase with predator size. Pelicans often take carp up to 68 cm (Hall 1925), thus supporting those studies. Our data on *G. bicolor* are not comparable, however, since they represent only a portion of the pelican diet.

Cormorants and pelicans exploited the *G. bicolor* population differently, apparently relative to their respective foraging techniques. Prior to spawning, *G. bicolor* forms large swarming schools at the lake's surface. Both bird species are attracted to the schools where they forage simultaneously. Cormorants dive and select only the larger chubs from schools, presumably offsetting the greater energetic costs of underwater pursuit. Pelicans remain at the surface and take available fish, capturing many smaller fish but with less effort.

The diet of cormorants at Pyramid Lake is likely opportunistic in that they cannot fly efficiently to outlying wetlands to forage, and must forage from the predominantly chub fish community. However, the cormorants' species- and size-specific diet is atypical relative to its food habits in other regions of North America (Robertson, Condor 76:346–348, 1974). Pelicans, also opportunistic, often fly great distances from nests to feed (Low et al., Auk 67:345–356, 1950; Lingle and Sloan, Wilson Bull. 92:123–125, 1980) and probably nest on Anaho Island since no other suitable islands for nesting occur in the area. The pelican exploits the large *G. bicolor* population when available, but does not demonstrate the reliance of the cormorant upon that fish species.

Piscivorous bird species reduce competition for food where they coexist by foraging on different sizes of fish, at different distances from nests, or by having non-overlapping breeding seasons (Cody, Ecology 54:31–44, 1973). We are uncertain whether cormorants and pelicans compete for *G. bicolor.* The potential for competition is high, since of the five fish species in Pyramid Lake, *G. bicolor* comprises 86% of all fish (by numbers) available to cormorants in water 0–15 m deep (Vigg, Calif. Fish and Game 66:49–58, 1980) and virtually all fish available to pelicans in water 0–1 m deep. The cormorant population appeared below the area's carrying capacity since cormorants historically nested also on rocky pinnacles jutting from the north end of the lake (Marshall and Giles, Condor 55:105–116, 1953) where 272 nest structures were present, but unused, 1976–1977.

We thank W. F. Sigler and Associates, Inc. for the opportunity to conduct this study. The Paiute Indian Tribe, PLITE, and the U. S. Fish and Wildlife Service extended permission to work on Pyramid Lake and Anaho Island NWR. L. Howard and M. Barber of the Stillwater Wildlife Management Area provided field assistance on Anaho Island. B. A. Knopf prepared the figure. S. F. Fox, E. A. Gluesing and P. A. Vohs commented on the manuscript.—FRITZ L. KNOPF, *School of Biological Sciences, Oklahoma State Univ., Stillwater, Oklahoma 74074* AND JOSEPH L. KENNEDY, *Dept. Biology, Western Montana College, Dillon, Montana 59725.* (Present address FLK: *U.S. Fish & Wildlife Service, Denver Wildlife Research Center, 1300 Blue Spruce Dr., Fort Collins, Colorado 80524-2098.*) *Accepted 8 Oct. 1980.*

Wilson Bull., 93(4), 1981, p. 557

Red Phalarope eating carrion.—The Red Phalarope (*Phalaropus fulicarius*) eats numerous invertebrate species and tiny fish outside the breeding season, and at sea (Bent, U.S. Natl. Mus. Bull. 142, 1927; Niethammer, 1942, *in* Birds of the Soviet Union, Vol. 3, G. P. Dement'ev, N. A. Gladkov and E. P. Spangenberg, eds., Israel Prog. for Sci. Transl., Jerusalem, 1969). In this note I describe the behavior of a Red Phalarope eating carrion, which is the first such record for this species.

On 11, 13 and 14 September 1978, I observed a Red Phalarope in first basic plumage, at the freshwater East Pond of Jamaica Bay Wildlife Refuge, New York City. Observations were made from a distance of about 15 m using 7 × 35 binoculars and a 15× spotting scope. The phalarope vigorously picked and pulled at the flesh surrounding the ribs and sternum of three different floating bird carcasses, while swimming actively around them. It spent most of its time at the carcasses of a Red Knot (*Calidris canutus*) and a Herring Gull (*Larus argentatus*). Both carcasses had the flesh exposed in the area of the sternum and body cavity; examination in the hand revealed no invertebrates on either carcass upon which the phalarope might have been feeding. Several other observers also saw the phalarope feeding on the same carcasses at other times during the same period.

Many other carcasses of shorebirds, gulls and waterfowl in various stages of decomposition were present but all were on land and all were unopened; the phalarope was never seen visiting them.

It seems unlikely that the Red Phalarope with its rather blunt bill could have opened the carcasses by itself and although the bird was often observed on land it may not have fed on carcasses on land because they were unopened. At the end of my observations very little meat remained on the carcasses, and the phalarope was observed feeding in typical phalarope fashion, presumably on aquatic invertebrates. This observation suggests that Red Phalarope could feed facultatively on carrion while at sea, an aspect of their feeding ecology previously unreported.

I thank Joanna Burger, Charles F. Leck and Sharon Ann Brady for comments on this note. This research was funded by a grant to J. Burger from the National Park Service.—Wade Wander, *Center for Coastal Environmental Studies, Rutgers Univ., Piscataway, New Jersey 08854.* (Present address: *RD3, Box 270AA, Somerset, New Jersey 08873.*) *Accepted 20 Aug. 1980.*

Wilson Bull., 93(4), 1981, pp. 557–559

Re-mating of a Lesser Snow Goose.—Mate selection and pair formation in most geese occurs during winter and spring (Delacour, Waterfowl of the World, Vol. IV, Country Life, London, England, 1964). Direct observation of the process in nature is difficult, but good evidence of winter pairing is provided indirectly by banding studies (e.g., Cooke et al., Auk 92:493–510, 1975). Exact timing of pair formation presumably depends on reproductive condition, availability of potential mates, previous pairing experience and perhaps social status. We describe events in the formation of a new bond by a female Lesser Snow Goose (*Anser caerulescens caerulescens*) immediately following mate loss and discuss their timing and significance.

Observations were made during May and June 1977, at La Pérouse Bay, Manitoba (58°45′N, 94°30′W), during the peak of nesting in a colony of Lesser Snow Geese. The female

involved nested 35 m from our live-in observation tower, and was identifiable by colored leg bands. Her mate was shot on 23 May 1977, on the third day of incubation. Subsequent behavior and movements of the female and her new "mate" were monitored opportunistically. In addition, during 39 one-h periods of instantaneous scan sampling (Altmann, Behaviour 49:227–267, 1974) over a 19-day period, time spent in alert, feeding, resting and maintenance activity was recorded.

General observations.—The female was sexually assaulted by neighboring territorial males (Mineau and Cooke, Behaviour 70:280–291, 1979) and harrassed by non-nesting pairs after her mate was shot. In the early morning of 25 May, between 32 and 41 h after the male's removal, she abandoned the nest and the eggs were preyed upon. Pairs searching for nest-sites, non-nesting pairs and yearlings all frequented the immediate vicinity of the nest between the time of the male's death and nest loss. Thus, we do not know when the yearling male which subsequently formed a bond with the female first visited the area. The behavior of yearlings while on the nesting colony suggests that he was present before and during the female's harassment. Although not banded, the yearling was recognizable by his distinctive plumage. We first noted his presence near the female at 07:55 on 25 May, within hours of nest loss.

Bond formation and sexual behavior.—Throughout 25 and 26 May the yearling chased the female. Both birds were on the ground and vocalizing during the chases. The female held her wings partially open at such times. The ground pursuits changed abruptly into aerial pursuits lasting less than 1 min, usually culminating with the birds landing together near the take-off point. In four of five fully observed sequences, both birds fed quietly after landing; in the first sequence seen, the male returned after the female, remained alert and fed later. These "courtship flights" were observed in decreasing frequency during the week after the first chase was seen. Prevett and MacInnes (Wildl. Monogr. No. 71, 1980) observed similar behavior by snow geese and reported its occurrence during winter and spring.

By 18:00 on 25 May, nesting pairs and other geese treated the female and yearling as a "pair," threatening them if they approached too closely to nests or other individuals. The new "pair" was not aggressive in these encounters at first and usually fled. However, late on 26 May, they began responding jointly to threats by assuming threat postures and rushing at other geese. We did not observe the two performing a triumph ceremony.

Copulation is an important pair bond reinforcement behavior in waterfowl (Delacour 1964). No complete copulations were observed but the male engaged in intensive bouts of pre-copulatory display on 27 and 28 May, and 8 June. The female ignored these displays except on 28 May when she briefly joined in typical pre-copulatory dipping. The male first displayed 3 days after nest loss, that is 7 days into the female's "incubation" stage. Mineau (M.Sc. thesis, Queen's Univ., Kingston, Ontario, 1978) noted that females of established pairs ignore their mates' sexual advances soon after incubation begins. Our failure to observe copulation by this pair probably reflects both the female's physiological condition and the infrequency of the event.

Throughout the first 10 days of the association, the male was more alert than the female (40.0% vs 23.4% of instantaneous scans) and fed less (53.8% vs 70.3%) ($\chi^2 = 9.49$, df = 1, $P < 0.01$). The frequency of rest and comfort behaviors did not differ significantly. After the first 10 days the frequency of each behavior did not differ between the two birds. Mapping of the pair's location at each scan sample (N = 269) showed that they were within 100 m of the female's destroyed nest on 75% of the scans. Distance from the nest increased gradually over the 19 days of observation. Neither goose was seen after 12 June; this last sighting coincided with a molt migration when most non-nesting snow geese left La Pérouse Bay.

The triumph ceremony is usually accepted as an absolute criterion for existence of a pair bond in geese. Although we did not observe this display, the consistent close proximity over 3 weeks, the coordination of behaviors and pair-pair interactions all indicated that a bond

of some sort existed. Because the mate selection process in geese may involve a series of temporary associations, the bond formed here need not have been permanent. However, Wood (J. Wildl. Manage. 29:237–244, 1965) reported that Canada Goose (*Branta canadensis*) pairs formed while at least one of the members is immature (as in this case) are as likely to persist as are those formed when both members are adult. In the spring of 1978, this banded female was observed nesting with a white male 80 m from her 1977 site, within the home range occupied by the newly formed "pair" in 1977.

Cooch (Ph.D. thesis, Cornell Univ., Ithaca, New York, 1958) assumed that pair formation of some snow geese began in their yearling summer; our observations confirm that possibility. Although bond formation such as we describe is likely to occur relatively infrequently, it runs counter to the assumption that all pairing occurs during winter and spring (Cooke and Sulzbach, J. Wildl. Manage. 42:271–280, 1978).

The reported length of the period between mate loss and re-mating in geese is variable. In our case, a bond of some sort was formed within 48 h. Re-mating before the next breeding season is common in snow geese (Cooke, unpubl.). Prevett and MacInnes (1980) reported that some snow geese remained unpaired in the breeding season after mate loss. Similar variability in interval from mate loss to re-mating has been reported for Canada Geese and is likely true for other species (Sherwood, Trans. N. Am. Wildl. Nat. Res. Conf. 32:340–355, 1967; Weigand et al., J. Wildl. Manage. 32:894–905, 1968; Jones and Obbard, Auk 87:370–371, 1970). Much of the variation can be explained by difference in time of mate loss relative to the next breeding opportunity and the availability of mates. Although a succession of temporary associations may usually be a part of the pair formation process in geese because it allows optimal discretion in choice of mate, circumstances may not permit. In particular, loss of mate during the nesting period characterized both cases where a new bond was formed within a very short time (Jones and Obbard 1970, this study). The male's important role in protection of the female and/or nest clearly favored the short interval (Ewaschuk and Boag, J. Wildl. Manage. 36:1097–1106, 1972; Mineau and Cooke, Wildfowl 30: 16–19, 1979). Mate loss at other times of the year could result in longer re-mating times because both need for a mate and availability of potential mates will differ.

Acknowledgments.—Funding for the La Pérouse Bay snow goose study was provided by the Canadian Wildlife Service, National Research Council of Canada and the Wildlife Management Institute. We thank M. A. Bousfield for assistance in the field and C. D. Ankney for comments on an earlier draft of the paper.—Kenneth F. Abraham, Pierre Mineau and Fred Cooke, *Dept. Biology, Queen's Univ., Kingston, Ontario K7L 3N6 Canada.* (Present address: KFA, *Dept. Zoology, Univ. Western Ontario, London, Ontario N6A 5B7 Canada;* PM, *Canadian Wildlife Service, P.O. Box 5050, Burlington, Ontario L7R 4A6 Canada.*) *Accepted 17 Nov. 1980.*

Wilson Bull., 93(4), 1981, pp. 559–560

Common Eider plays "possum."—Death feigning is widespread but not extensively described in animals. Reports of death feigning in birds are given by Armstrong (Bird Display and Behavior, Dover Publ. Co., New York, New York, 1965), Vogel (Auk 67:210–216, 1950), Francq (Am. Midl. Nat. 81:556–568, 1969), and others. Observations of invertebrates and vertebrates indicate that it is used only when escape is otherwise impossible and that it appears to be a stereotyped response.

At 13:30 on 17 January 1979, at Great Island, Wellfleet, Barnstable Co., Massachusetts, I observed an ill adult female Common Eider (*Somateria mollissima*) feigning death. My dog

found it on slush tidal ice 8 m from a salt marsh channel and 28 m from open water. The eider hobbled weakly away and beat the ground with its wings then slumped into immobility when the dog came alongside it. The eider's head and bill were depressed until the tip was 3 cm above the ground. The neck was twisted, body slumped forward, wings folded and tarsi tucked under the body. The bird remained motionless as the dog wandered no more than 5 m away. Closer inspection revealed breast, belly, flanks and undertail coverts were saturated with water. Ventral feathers around the cloaca were stained green, suggesting either lead poisoning or botulism; grit was also concentrated around the cloaca. The eyes were open but "glassy"; they were rolled and exposed much white. The nictitating membrane was not observed to function, and an eye did not respond when I touched it. I twisted the neck, pulled feathers on the back and wings, tapped head and bill with my fingers, let the head and bill drop 4 cm on the ice, and still observed no response. I did not feel the bird breathing. The only sign of life was involuntary pedalling of the tarsus and feet when I inverted the eider. I released it 2 m from open water and walked away 20 m. It remained on the ice in a death-feigned posture for barely 1 min. The head and neck came up suddenly and it appeared to look in our direction. My dog pursued it but the eider escaped to the water, where it preened vigorously and then slowly swam toward shore.

Perry (1938, *in* Armstrong 1965) described death feigning in a male eider which was apparently in good health. Armstrong (1965) records death feigning and injury distraction in a nesting adult female Greater Golden Plover (*Pluvialus apricaria*) suggesting association of these responses. Operational definitions of death feigning, immobility and "freezing" are lacking. Relationships of immobility responses to "freezing" postures have not been investigated (Hinde, Animal Behavior, 2nd ed., 1970:420). Laboratory studies conducted by Rather and Thompson (Anim. Behav. 8:186–191, 1960) and Francq (1969) suggest the response develops at the period of emerging physical independence, not sexual maturation. Death feigning may be a response to extreme stress. However, Norton et al. (Nature 204:162–163, 1964), studying brain wave recordings in immobile opossums (*Didelphis virginianus*) during "feigned sleep," found no changes between "feigned" and normal states; the animals maintained normal brain wave patterns and heart rates, suggesting the state of shock in the animal is erroneously assumed.

Controlled experiments are needed to define the relationship of death feigning to other similar respones. Natural observations can do little more to provide evidence of the mechanisms of these relationships. Death feigning has survival value to the individual and has almost certainly evolved through natural selection.

Thanks to R. M. Alison and J. Jackson who were very helpful referees.—Douglas B. McNair, *Dept. Biological Sciences, P.O. Drawer GY, Mississippi State Univ., Mississippi State, Mississippi 39762.* (Present address: *Dept. Zoology, Clemson Univ., Clemson, South Carolina 29631.*) *Accepted 22 Sept. 1980.*

Wilson Bull., 93(4), 1981, pp. 560–561

Territorial attachment and mate fidelity by Horned Grebes.—Although territorial attachment has been documented for many migratory birds (see Austin, Bird-Banding 20:1–39, 1949; Hilden, Ann. Zool. Fenn. 2:53–75, 1965), evidence that grebes (Podicipedidae) return to the same nesting territory in consecutive years is largely circumstantial. This note documents territorial attachment and mate fidelity by individually marked Horned Grebes (*Podiceps auritus*) at Minnedosa, Manitoba (50°15′N, 99°50′W). Seven of 50 grebes (43 adults and seven juveniles) banded in 1974 and 1975 were recaptured in either 1975 and 1976 by using

a submerged gill net (Ferguson, J. Field Ornithol., 51:179–180, 1980). Whether any of the other banded birds returned was not determined. Each pair of grebes mentioned in this note occupied an entire pothole marsh as its territory. Territorial attachment means an individual's return to the same nesting territory. Mate fidelity is defined as breeding with the same mate for more than one breeding season.

Five of the seven recaptured grebes (three males and two females) nested on territories on which they had nested and raised young to fledging in the previous year. On 25 May 1976, I recaptured both members of a nesting pair (pair 20) which had fledged young from the same pond in 1975. Both birds had been banded as adults on this pond on 10 June 1975. Their recapture illustrates both territorial attachment and mate fidelity. Fjeldsa (Sterna 12:161–217, 1973) suggested that mate fidelity by Horned Grebes in Sweden may be due to a sustained monogamy. At Minnedosa, this is unlikely in view of the pattern of summer departure of adults. In 1975, the male of pair 20 left the territory between 2 and 7 July, leaving its mate and two unfledged young. The female deserted the territory between 19 and 23 July, at least 12 days after the male had departed. This pattern of dispersal from territories was typical of adult grebes unless a pair attempted to raise a second brood (Ferguson, M.Sc. thesis, Univ. Manitoba, Winnipeg, Manitoba, 1977). Renewal of a pair-bond probably occurs in the following spring (as with pair 20 in 1976), facilitated by territorial attachment. Both sexes demonstrated an attachment to former nesting territories as shown by the following examples.

Two males banded as adults on 1 and 6 June 1975, were recaptured on the same territories on 31 and 25 May 1976, respectively. At least one of these males was paired with a different mate in 1976. This male, whose original mate had been banded in 1975, was paired with an unmarked female in 1976. On 3 June 1975, a nesting female was recaptured on a pond on which she had raised young in 1974. She had been banded as an adult on 19 June 1974. I was unable to capture and band her mate in either year.

Migrational homing, defined as the return of individuals to the same nesting area (Dwyer, Derrickson and Gilmer, Auk 90:687, 1973), was documented for two males. On 10 June 1975, a nesting male banded as an adult on 2 July 1974, was recaptured on a pond 3.7 km from his former nesting territory. A second male, banded on 1 July 1974, was recaptured on 24 May 1976, on a pond 0.8 km from his 1974 nesting territory. This male was not observed during 1975. I found no evidence of Horned Grebes returning in their first breeding season to their natal ponds. However, this was inconclusive considering that only seven juveniles were banded.

In summary, it is doubtful that mate fidelity by Horned Grebes is due to year-round pairing. Alternatively, territorial attachment by both sexes may result in contact with former mates and in an opportunity for renewing pair-bonds in spring. Behavioral evidence suggests that some pairing occurs on the breeding grounds (Ferguson 1977). By returning to nest at familiar marshes where nesting was previously successful, grebes may increase both their chances of survival and of raising young. At Minnedosa, ponds which supported a pair that fledged young were occupied more frequently in the following year (8 of 18 ponds) than ponds which initially supported a pair that failed to raise young (2 of 21 ponds).

Financial support for fieldwork was provided by the National Research Council of Canada and the Northern Studies Committee of the Department of Indian and Northern Affairs (grants awarded to S. G. Sealy, University of Manitoba), Gulf Oil Canada Limited, Manitoba Department of Renewable Resources and Transportation Services and National Audubon Society. Banding permits were kindly provided by the Canadian Wildlife Service. I am grateful to S. D. MacDonald and K. S. Yonge for commenting on an earlier draft of the manuscript.—ROBERT S. FERGUSON, *#402 112–111 Street, Saskatoon, Saskatchewan S7N 1S7 Canada.* *Accepted 25 Aug. 1980.*

Wilson Bull., 93(4), 1981, pp. 562–563

Effects of Redhead nest parasitism on Mallards.—Female Redheads (*Aythya americana*) are known to deposit eggs in nests of Mallards (*Anas platyrhynchos*). Joyner (J. Wildl. Manage. 40:33–38, 1976) attributed a high rate of Redhead parasitism on Mallard nests at Farmington Bay, Davis Co., Utah, to crowding of host and parasite into the same habitat. Weller (Ecol. Monogr. 29:333–365, 1959) stated that at Knudson Marsh, Utah, only a few deep channels and patches of water were suitable for feeding and courtship by Redheads, and nests of other ducks located near those areas were heavily parasitized; nests farther from the shore were parasitized less often. Redhead nest parasitism resulted in reduced host clutch-size (Weller 1959), displaced and broken host eggs (Joyner 1976) and increased nest abandonment (Ryder, Trans. N. Am. Wildl. Nat. Resour. Conf. 26:134–146, 1961).

Although the Prairie Pothole Region of North America is the principal breeding ground of both species, little is known concerning the extent and effects of Redhead parasitism on Mallards. Because the Mallard commonly nests in marshes in the Prairie Pothole Region (Krapu et al., Wildl. Soc. Bull. 7:104–110, 1979), potential exists for high levels of nest parasitism. This paper describes the effects of nest parasitism by Redheads on Mallards that nested in marshes in south-central North Dakota.

Data were collected on the Medina Study Area (93.2 km²) in western Stutsman County, North Dakota. The study area, located within the Missouri Coteau, is moderately rolling glacial moraine containing 2–14 wetlands per km². A detailed description of the study area was presented by Krapu et al. (1979). In 1976 and 1977, wetlands were searched for Mallard nests by systematically wading through emergent vegetation. A colored flag was placed 6 m from each nest; nests were periodically revisited until the eggs hatched or until the nests were abandoned or destroyed.

Of 24 active Mallard nests located in emergent vegetation of semipermanent marshes during 1976, 10 were parasitized by Redheads and two by Ruddy Ducks (*Oxyura jamaicensis*); one nest was parasitized by both species. In 1977, when water levels in semipermanent marshes were low because of a drought, only three nests were located, and we observed no interspecific nest parasitism. Therefore, all calculations were based on our 1976 data. Because nest parasitism by Ruddy Ducks was infrequent, we ignored the nest parasitized solely by a Ruddy Duck and based our calculations on the remaining 23 Mallard nests.

Success rates of parasitized and unparasitized nests (4 of 10 [40%] and 3 of 13 [23%], respectively) were not significantly different ($\chi^2 = 0.77$, df = 1, NS). Unparasitized nests and those parasitized by Redheads were abandoned at similar rates (4 of 13 [30.8%] and 3 of 10 [30%], respectively). Additionally, the percentages of parasitized and unparasitized Mallard nests destroyed (3 of 10 [30%] and 6 of 13 [46.2%], respectively) by predators were not significantly different ($\chi^2 = 0.62$, df = 1, NS).

Redhead nest parasitism resulted in significantly fewer Mallard eggs per nest ($t = 9.71$, df = 21, $P < 0.05$). The mean number of Mallard eggs in nests parasitized by Redheads was 5.6 ± 2.2 compared to 7.2 ± 3.1 eggs in unparasitized marsh nests. Also, in nests that hatched at least one egg, Mallard egg success in parasitized nests was significantly lower than success of eggs in either unparasitized marsh nests ($\chi^2 = 6.83$, df = 1, $P < 0.05$) or unparasitized upland nests ($\chi^2 = 6.40$, df = 1, $P < 0.05$) monitored on the study area (Table 1). Mallard egg success in parasitized marsh nests was only 43%, whereas success in unparasitized marsh nests was 80%. Thus, the primary effects of parasitism were a reduced number of Mallard eggs in nests and lowered egg success.

Egg success at parasitized nests was decreased by a combination of factors; egg displacement was the most important. Thirty-five percent of the Mallard eggs in parasitized successful nests were displaced from nests. Most displaced eggs were under water near the

Table 1
Comparative Egg Success in Parasitized and Unparasitized Successful Mallard Nests on the Medina Study Area in 1976

Habitat	Total eggs		Eggs hatched	
	Host	Parasite	Host	Parasite
Unparasitized				
Upland	50	—	37	—
Marsh	25	—	20	—
Parasitized				
Marsh	23	20	10	8

nests. Infertility and death of embryos, primarily because of cracked eggs, caused most other egg losses.

Egg deposition by Redheads often preceded incubation by Mallards and may have suppressed ovulation in Mallard hens. The comparable hatching success of host and parasite eggs (Table 1) indicated that many parasitic eggs were deposited in Mallard nests before incubation began. On average, 3.8 Redhead eggs were deposited in each parasitized Mallard nest, and 1.5 Redhead ducklings hatched from each successful parasitized nest. This occurred when densities on the study area were about four pairs of Redheads per km^2 and three pairs of Mallards per km^2 (A. D. Kruse, unpubl.).

Our data suggest that Redhead nest parasitism reduces the number of Mallard ducklings hatched at marsh sites in the Prairie Pothole Region. Presumably, the extent of Redhead nest parasitism varies with water conditions, densities of parasite and host, and the relative number of Mallards nesting in marsh habitat. Because Mallards commonly nest in marshes, potential exists for substantial Redhead nest parasitism and attendant reduction in number of Mallard eggs per nest and egg success. However, additional research is needed to evaluate this potential.

Acknowledgments.—The study was supported by the Northern Prairie Wildlife Research Center (Contract No. 14–16–0003–2038) and conducted under the auspices of the Oregon Cooperative Wildlife Research Unit; Oregon Department of Fish and Wildlife, Oregon State University, U.S. Fish and Wildlife Service and Wildlife Management Institute cooperating. Oregon State University Agricultural Experiment Station Technical Paper No. 5406.

We thank J. A. Crawford and J. R. Serie for critically reviewing the manuscript; D. G. Jorde, L. Kludt, and R. Green for assisting with collection of data; and S. D. Becker for helping locate Mallard nests.—Larry G. Talent, *Oregon Cooperative Wildlife Research Unit, Oregon State Univ., Corvallis, Oregon 97331,* Gary L. Krapu, *U.S. Fish and Wildlife Service, Northern Prairie Wildlife Research Center, Jamestown, North Dakota 58401* and Robert L. Jarvis, *Dept. of Fisheries and Wildlife, Oregon State Univ., Corvallis, Oregon 97331.* (Present address LGT: *Dept. Zoology, Oklahoma State Univ., Stillwater, Oklahoma 74078.*) *Accepted 14 Oct. 1980.*

Wilson Bull., 93(4), 1981, pp. 563–565

Survival of a demaxillate Red-winged Blackbird.—The literature contains numerous reports of birds with abnormal bills. Surprisingly, in view of the supposed adaptiveness of

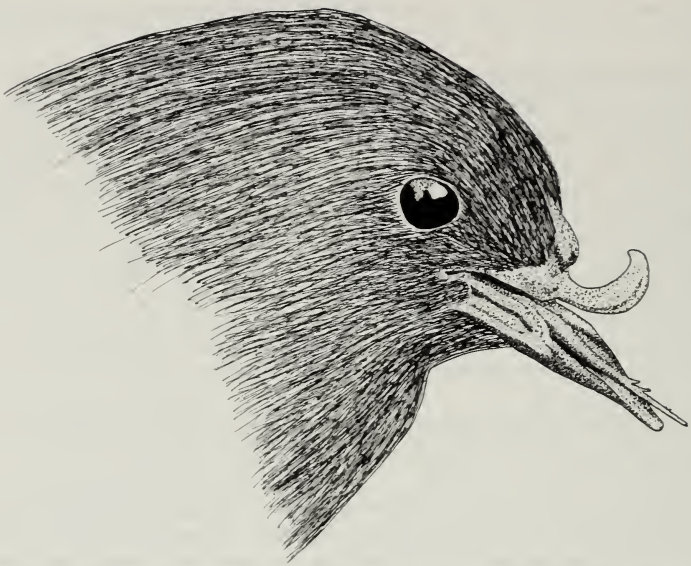


FIG. 1. Red-winged Blackbird with abnormal bill; drawn from photograph taken 16 April 1977.

bill structure, such birds often appear to have adjusted successfully to their deformity, judging from their apparent good health at the time of collection or observation or from the apparent long standing of the deformity by the time it is noted. However, confirmations of long-term survival are few; I have found only five reports of survival for a year or more (Stamm, Kentucky Warbler 49:75, 1973; Donark, Dansk Ornithol. Foren. Tidsskr. 44:16–19, 1950; Nowak, Der Falke 12:122–130, 1965; Pomeroy, Br. Birds 55:49–72, 1962; Wystrach, Auk 94:781–782, 1977). I report the survival for at least 3 years of a male Red-winged Blackbird (*Agelaius phoeniceus*) that lacked most of its maxilla.

I first trapped the bird, then in subadult plumage, on 25 May 1976, at the University of Michigan's E. S. George Reserve, Livingston Co., Michigan. The stump of its maxilla extended to the middle of the nostrils, which had become closed, forcing the bird to breathe through its mouth. The normal structure of the base of the maxilla suggested that the loss was the result of an accident (perhaps with a spring-type rodent trap; I have seen an American Robin [*Turdus migratorius*] so caught) rather than a congenital defect. The tongue was normal and the mandible complete, but the tomia were slightly hypertrophic. The bird's weight (68.0 g) was normal, and it was in vigorous condition. Although I happened to observe the bird arrive at the corn-baited trap and feed briefly before becoming caught, its behavior was not unusual and I noticed the abnormality only after retrieving the bird. I banded and released it, but did not observe it again that year.

On 11 March 1977, and on the next few days, I saw the same bird singing in woods on the George Reserve. The area in which it sang adjoins areas annually occupied by territorial males, but does not itself contain suitable nest-sites, and the bird did not remain there. At this time the bird had a recurved horny outgrowth from the ventral side of the maxilla (Fig. 1). I trapped it again on 16 April 1977, and found it still in good condition, weighing 71.8 g,

but about 12 ectoparasites crawled onto my hand as I held it. This has not occurred on any of a few hundred captures of adult males with normal bills. At this capture the bird received a unique color-band combination. I observed it once more that year, on 13 June, in an area where a flock of males was beginning to congregate. By then it had lost the horny outgrowth.

I again observed the bird on 7 May 1978, when it intruded briefly into the territory of another male. On several occasions from 28 July–13 August 1978, it appeared with other males feeding on cracked corn on the lawn under my feeding tray. It picked up the corn from among blades of grass with as much facility as the other birds, scooping up a grain with the mandible then manipulating it at the base of the bill as do normal birds. Its behavior was sufficiently normal that, although I was only 5 m distant, I recognized the bird by its color bands sooner than by its bill.

My final observation of the bird was on 24 March 1979, when it briefly visited the trapping station. I did not specifically note its bill on this occasion and identified the bird only after a later check of the color bands.

Bill structure is usually associated most closely with survival aspects of fitness, but it probably has indirect effects on reproductive success as well. Unfortunately, I have no information on this bird's reproductive success. During the four breeding seasons in which I observed the bird I was studying the redwings breeding in the marshes near the trapping site and would have found its territory had it had one there. However, there are numerous other marshes slightly more distant where it could have had a territory.

I thank A. Martin for editorial suggestions.—Kent L. Fiala, *Museum of Zoology, Univ. Michigan, Ann Arbor, Michigan 48109.* (Present address: *Dept. Ecology and Evolution, SUNY, Stony Brook, Long Island, New York 11794.)* *Accepted 24 Nov. 1980.*

Wilson Bull., 93(4), 1981, pp. 565–569

Minimizing investigator disturbance in observational studies of colonial birds: access to blinds through tunnels.—Colonial nesting birds present unique advantages and disadvantages to the investigator of behavior and ecology. A major advantage is that there are many birds concentrated in a relatively small area, which allows accumulation of large data sets. A disadvantage is that investigator disturbance can bias or affect efficiency of data collection, particularly if birds in a colony are not accustomed to humans. Investigator effects can range from simple disruption of ongoing breeding activities and colony dynamics (Vermeer, Can. Wildl. Serv. Rept. Series 12, 1970; Smith, Br. Birds 68:142–156, 1975; Sears, Bird-Banding 49:1–16, 1978) to chick mortality as young run from their territories and become lost or are killed (Emlen, Wilson Bull. 68:232–238, 1956; Ashmole, Ibis 103b:297–364, 1961; Kadlec and Drury, Ecology 49:644–676, 1968; Kadlec et al., Bird-Banding 40:222–232, 1969; Roberts and Ralph, Condor 77:495–499, 1975; Gillet et al., Condor 77:492–495, 1975; Davies and Dunn, Ibis 118:65–77, 1976). Predacious gulls (*Larus* spp.) also may take advantage of the disturbance and eat eggs and chicks of their own and other species nesting in or near the same colony (Kury and Gochfeld, Biol. Conserv. 8:23–34, 1975; Ellison and Cleary, Auk 95:510–517, 1978). These disturbance related effects are inherent in studies conducted from observation blinds placed within nesting colonies simply because the investigator creates a disturbance while entering a blind. To minimize unwanted disturbance and related effects in sparsely vegetated Lake Michigan bird colonies, we have designed and used an easily constructed tunnel system which permits access to blinds.

Methods and materials.—The design described here was used in 1978 and modified in

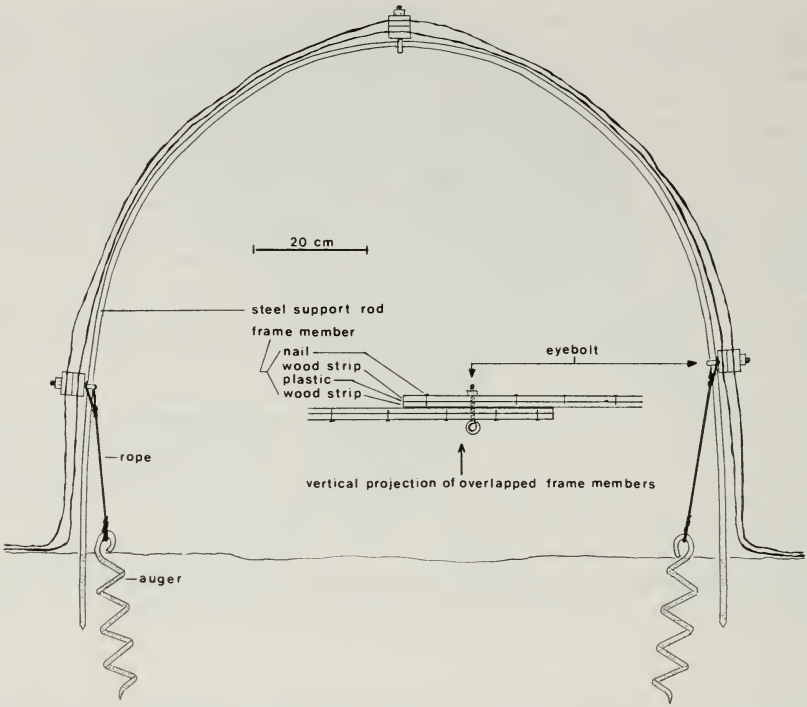


FIG. 1. Cross section of tunnel showing details of construction where two tunnel sections join; drawn to scale.

1979 to withstand high winds. The tunnel described in this paper is the one used in 1979 unless otherwise noted. Modifications can be made depending on conditions unique to the investigator's study area and species.

The tunnel consisted of 3.1 m (10 ft) × 2.4 m (8 ft) black plastic sheets that were attached to 9.5 mm (0.375 in) × 38.0 mm (1.5 in) × 3.1 m (10 ft) wooden strips (Figs. 1, 2). English equivalents are provided to facilitate purchasing of material.) Sections of tunnel were prefabricated by nailing two wood strips together with the plastic sandwiched between at the center of each 3.1 m length of plastic (Fig. 2). At 0.8 m (2.5 ft) on either side of the center of each 3.1 m length of plastic, two more strips were nailed together. This resulted in three wooden frame members 19 mm 0.75 in) × 38.0 mm (1.5 in) per tunnel section.

We formed the tunnel by joining the three frame members from each section end-to-end with frame members from another section (with 0.2 m overlap) using eyescrews or eye-bolts (Figs. 1, 2). Frame members were pre-drilled to save time in the field if eye-bolts were used. Metal supports for the plastic sections were 2.4 m (8 ft) lengths of 6 mm (0.25 in) steel rod bent in a U-shape. Tunnel erection initially consisted of threading a metal rod through the eyes, standing the metal support rods with ends down, forcing the ends of the metal rod into the substrate, and spreading the plastic over the metal frame.

The end-to-end attachment of tunnel sections created uneven overlaps of the frame members when sharp changes of direction or elevation were attempted. When such angular

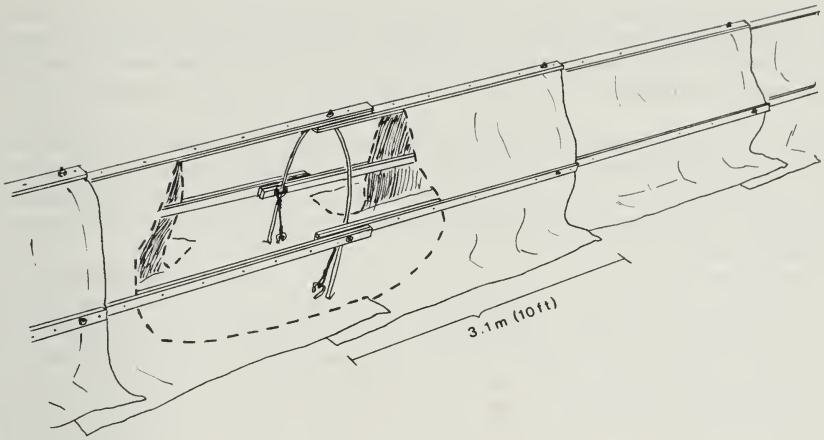


FIG. 2. Plastic removed from a portion of the tunnel (dotted line) to show construction details; drawn to approximate scale.

changes were necessary we simply lashed the wooden frame members to the metal frame after compensating for the uneven overlap.

After initially setting the tunnel up and adjusting the plastic, we entered the tunnel and attached it to the ground with augers that we had pre-formed by twisting 0.6 m (2 ft) sections of 6 mm (0.25 in) steel rod around 24 mm (1 in) diameter soil-pipe. Two augers were twisted into the ground at each hoop, and the eye-bolt was tied to the auger (Fig. 1). Additional augers or conventional stakes were added midway between hoops and the frame members were tied to these. Augers were used because of superior holding power in sand, cobble, and gravel as compared with conventional stakes. They also were easier to manipulate inside the tunnel. Staking the tunnel down from inside reduced disturbance to incubating birds during tunnel erection.

Results and discussion.—We bolted five sections (15 m) of tunnel together outside the colony, threaded the rods through the eyes and carried six 15-m lengths of tunnel into position. Bolting the sections together took about 3 h and moving them into position and initial erection took approximately 1 h. Six hours were required to securely stake the tunnel from the inside. When completed the tunnel was approximately 1 m wide at the base and 1–1.2 m high. A 2 m tall human could easily crawl the 90 m length with a 10 kg pack around the neck in a few minutes.

The tunnel entrance was located in the shrub and tree covered island interior where we entered without being seen by birds. The tunnel passed 90 m through a Herring Gull (*Larus argentatus*) colony and terminated in a blind adjacent to a Caspian Tern (*Sterna caspia*) colony. A Herring Gull observation blind was also placed at the midpoint.

Moving through the tunnel created a peristaltic-like movement of the plastic sheet. Since the plastic flapped and fluttered in the wind, birds did not notice our passing on windy days. On calm days, gulls standing on top of the tunnel or adjacent to it gave low intensity alarm calls when we passed. In contrast, all birds within 100 m took to the air when a human emerged from the vegetation and walked to a blind.

In both seasons, the tunnel was unprotected from winds. Since the plastic covering presents a large surface area to the wind, the wood and metal frame was subjected to consid-

erable stress. In 1978, this caused problems when smaller diameter rods (3 mm or 0.125 in) were bent out of shape and narrower wood strips (19 mm or 0.75 in) were broken by gales in excess of 60 kph. With 6 mm (0.25 in) rods and 38 mm (1.5 in) frame members in 1979 neither problem recurred. The tunnel withstood five gales, each of which blew for 24 h or longer.

Three frame members per section were used to minimize weight and cost. The plastic tended to sag in between frame members, but this did not necessitate the addition of another frame member on each side. Placement of the side frame members at 0.8 m (2.5 ft) from the center left a 0.5 m (1.5 ft) skirt that allowed ventilation, reduced wind stress and permitted young gulls to enter and exit.

We used 4 and 6 mil plastic in 1978 and 1979, respectively. In both years, Herring Gulls pecked and tore the plastic to such an extent that it had to be replaced or repaired on 50% of the sections. The 6 mil plastic used in 1979 apparently fatigued in the wind or sun and tears began appearing after 3 months exposure. The 4 mil plastic used in 1978 retained its resiliency through 1979. Reasons for the different wear characteristics apparently were related to different composition.

Preliminary evaluation.—Is the tunnel worth the effort? We can provide an initial assessment based on observations of Caspian Terns by Shugart and Herring Gulls by Fitch.

During 1977 through 1979 breeding seasons, Shugart observed individually marked Caspian Terns during the last part of incubation until after young could fly. An observation blind was approximately 10 m from the study area in each year. During this period in 1977, Shugart entered the blind one day and exited the next, creating one brief disturbance per day. Eight (of 8) marked pairs and their young moved at least 50 m away from the blind by the time the oldest study chick was 10 days of age. Observation of these individuals was terminated at this time because the birds were too far away from the blind to be seen clearly. It appeared that the movement away from the observation blind in 1977 was due to disturbance (see also Smith 1975, Sears 1978). In 1978, to minimize this possible effect on colony dynamics and to increase the period that marked individuals could be observed, Shugart alternated 5-day periods in the blind and 2 days out after the first study chick was 4 days old. In 1978, between the times Shugart left the blind and returned 2 days later, 2 of 22 (10%) study chicks were lost, and 3 of 12 (25%) family groups moved too far away to been seen clearly. We assume that the chick loss and movement were affected by exiting and entering disturbances as no movement or chick loss occurred after the birds had calmed down during the 5-day periods in the blind.

In 1979, tunnels were erected during late incubation and used to enter and exit the blind after the oldest study chicks were 4 days old. This permitted daily entering and exiting with minimal disturbance and observation of a near normal colony. Of 15 family groups marked, 14 centered activities at their natal site until at least 1 week after young could fly. The remaining family group moved from 10 m to within 3 m of the blind where they remained until after the young could fly.

Fitch's Herring Gull studies during 1977–1979 required placement of blinds throughout a colony to allow observation of widely spread polygynous groups. At blinds where tunnels were not used, the disturbance Fitch caused by walking through the colony to a blind indirectly resulted in chick mortality as the young ran from their territories and were killed by neighbors. Four of 10 (40%) chicks from two of four polygynous groups were killed in this way (Fitch, pers. obs.). Fitch observed 14 groups (monogamous and polygynous) from blinds that were entered by tunnels, and no chick mortality occurred due to entering blinds.

The disturbance-related effects on Caspian Terns and Herring Gulls that we have observed may not be important in all studies, but they were in ours. Movement of Caspian Tern families away from blinds reduced or eliminated the small sample of marked individuals,

and altered relationships between families as the remaining birds shifted to fill in vacated areas. In Fitch's study, the dispersion of polygynous groups made possible the observation of only a few polygynous groups per year. When chicks were lost from these groups differences in reproductive success and behavior between and within polygynous and monogamous mating types were masked or biased.

Although investigator disturbance and associated effects probably cannot be entirely eliminated, we feel it is best to conduct observations under conditions which are as natural as possible. This is particularly important when attempting to generalize reproductive and behavioral data taken from the necessarily small sample sizes that detailed observations require. It is also of importance when investigators attempt to assess inter-individual differences in reproduction and behavior.

We thank the Frank M. Chapman Memorial Fund for financial assistance to MAF during the study, T. O. Lempke for assistance in prefabrication of the tunnel sections, and J. R. Crook and B. G. Murray, Jr. for evaluating the manuscript.—Gary W. Shugart, Mary A. Fitch, *Ecology Program Bldg. 4087-Kilmer, Rutgers Univ., New Brunswick, New Jersey 08903* and Vern M. Shugart, *620 West Front St., Traverse City, Michigan 49684.* *Accepted 29 Sept. 1980.*

REQUEST FOR ASSISTANCE

Study collection.—Bird study skins, skeletons and alcoholics (world) are wanted for undergraduate and graduate ornithology collection. Labelled and unlabelled specimens sent collect shall be greatly appreciated and acknowledged in the collection. Contact John P. Ryder, Dept. Biology, Lakehead University, Thunder Bay, Ontario P7B 5E1 Canada. (807) 345-2121.

Wilson Bull., 93(4), 1981, pp. 570–574

ORNITHOLOGICAL LITERATURE

BREEDING BIOLOGY OF THE EGYPTIAN PLOVER *Pluvianus aegyptius*. By Thomas R. Howell. Univ. Calif. Publ. Zool. Vol. 113, Univ. California Press, Berkeley, California, 1979:76 pp., color frontispiece, 15 black-and-white plates, 6 numbered text figs., 5 tables. $10.50.—The Egyptian Plover, which is not a plover and no longer occurs in Egypt, has been an ornithological enigma fraught with the uncertainties attendant to a largely anecdotal and embellished literature. This courser (Cursoriinae, Glareolidae) figures in the textbooks as the reputed symbiont that gleans food particles from between the teeth of crocodiles (*Crocodilus niloticus*) and as a species whose buried eggs are incubated by solar heat. To our good fortune, a keen student of "avian adaptations that contribute to reproductive success in difficult and unusual environments" has conducted the first detailed field investigation of the species. The work was carried out on the Baro River at Gambela, Ethiopia from 24 January–6 April 1977, and this publication is the fascinating product of these efforts.

The principal subject of the research is evident from the title; the plover-crocodile association was only of minor concern. Nonetheless, Howell provides a brief but informative historical review of the latter, commencing with Herodotus who visited Egypt in 459 BC and "wrote of a bird called the Trochilos" which foraged inside "the gaping mouths of basking crocodiles." Although Howell never observed this behavior, he concludes from the published evidence that it probably occurs, and that it "may have been more frequent and widespread in earlier times, when both crocodiles and Egyptian Plovers were common all along the Nile." The interesting point is made that Herodotus' Trochilos cannot be identified with certainty as the Egyptian Plover; it may have been one of the spur-winged plovers (*Hoplopterus* sp.) or some other species.

Any sense of disappointment that the question of plover-crocodile symbiosis was not resolved once and for all is overwhelmed by the wealth of information on breeding biology contained in the remainder of the publication. Moreover, Howell's presentation is so logically structured and devoid of prolixity that a thoroughly lucid exposition of a large amount of data is packed within a relatively short monograph. Much of the data concern the remarkable egg-burying behavior of the Egyptian Plover which is central to a number of ecophysiological and behavioral adaptations of the species. The salient points are described below.

The eggs (usual clutch is 2 or 3) are laid in a scrape and kept covered with sand (to a depth of 2–3 mm above their upper surfaces) during the day. Adults toss the sand over the eggs with their beaks. Howell quantified the thermoregulatory parameters of nesting behavior by simultaneously recording nest temperatures (using thermocouple-implanted eggs) and relevant ambient termperatures. The pattern which emerged demonstrated that incubation is a "balanced combination of body heat, solar heat, and heat retained by the sand." During the periods from sunrise to about 10:00 and from about 16:00 to sunset, the latter two heat sources incubate the eggs, allowing the adults time to rest and feed. During the hottest part of the day (approximately 10:00 to 16:00) the eggs are in imminent danger of being overheated and solar input must be moderated. Simple shading of the nest is inadequate; instead the adults make frequent trips to the nearby river where they soak their ventral feathers, then quickly return and settle on the nest thereby moistening the eggs and surrounding sand. The resultant evaporative cooling keeps the eggs below lethal temperatures. Somehow the adults monitor nest temperatures (possibly with the beak), and their behavior varies accordingly. On cloudy days, for example, they stop wetting the eggs and regulation of nest temperatures is through other behaviors, such as varying the depth of the sand cover and/or settling on the nest. With the chill of night, an adult scrapes the sand (using its feet) away from the eggs and incubates them with the direct application of body heat. After hatching, the egg-

burying and nest-wetting behaviors carry over to the chicks. The latter are highly precocial and respond to potential danger by flattening themselves on the ground whereupon the adults cover them with sand. The chick-burying habit appears to be unique among birds, and is often so thorough that an observer cannot find them. While buried, the young are frequently wetted by the adults. This has significance in meeting the thermal stresses of early life, especially during the hottest hours of the day. The foregoing behaviors are nicely illustrated by accompanying plates.

Since Egyptian Plover eggs are small (9.5 g) relative to body weight (78 g) and incubation is protracted (30 days), Howell devotes a considerable portion of the monograph to the physiology of incubation. He hypothesizes that a lengthy period of incubation is "adaptively advantageous" since it produces a highly precocial chick able to survive in a difficult environment, and that the nest-wetting habit allows the small egg to withstand extended incubation without excessive dehydration.

The text is replete with a well-reasoned evolutionary theme concerning the adaptive values of the Egyptian Plover's breeding habits. Howell also uses his findings in an interesting "attempt to reconstruct the phylogeny" of the species. This outstanding monograph merits the attention of most avian biologists.—Oscar W. Johnson.

The Peregrine Falcon. By Derek Ratcliffe. Illus. by Donald Watson. Buteo Books, P.O. Box 481, Vermillion, South Dakota 57069, 416 pp., 4 color plates, 60 black-and-white photographs, numerous drawings, 16 numbered text figs., 23 tables. $42.50.—This is a detailed account of the biology of the British Peregrine Falcon (*Falco peregrinus*), surely the most thoroughly studied population of this species in the world. Major chapters are devoted to distribution, abundance, food, breeding behavior, population regulation and dynamics, and to man-caused impacts endured by the bird in historical times. The author claims the book has "no pretentions of scientific sophistication." Nevertheless, the vast data are exhaustively presented in table form and are tightly reviewed.

Ratcliffe has gone far beyond his own experience with the peregrine and provides a perspective based on both the formal and casual observations of hundreds of people. The book is probably the best single way yet to find out what peregrines are all about.

This book leaves the reader with two major impressions. One is the thoroughness with which the author and his many co-workers have recorded field data on over 950 eyries in England, Scotland and Wales. The other is the remarkable resiliency shown by peregrines in habitat so populated by people with varied interests in the bird. Falconry, first practiced by the Saxons in the 9th Century, flourished into the 1800's. Peregrine territories apparently remained at an upper numerical limit despite protection by nobility in that period. Between 1770 and the Second World War gamekeepers destroyed large numbers of peregrines, mainly on behalf of the Red Grouse (*Lagopus lagopus*). In one small locality alone in Scotland, 98 peregrines were killed between 1837 and 1840. Egg collectors, first active about 1840, took several hundred clutches in England such that few young fledged in some districts between 1900 and 1960. Between 1925 and 1959 racing pigeon fanciers waged war on peregrines. As before, immigration from more remote areas prevailed and territory occupancy was little affected. From 1939–1945 the Air Ministry organized destruction of nests to protect carrier pigeons, resulting in a brief 13% decline of the national peregrine population. Pesticides created a more severe reduction. Compounds such as dieldrin apparently increased adult mortality, and coupled with DDE-related egg breakage, evoked a population crash to 44% of pre-war numbers in the period 1955–1964. Following a ban on dieldrin and greatly reduced use of DDT, the population had increased to 75% of the pre-war level by 1979. The author

meticulously unravels these events, accounts which give cause for some optimism concerning reduced peregrine populations elsewhere.

Ratcliffe focuses on the British bird but provides a listing of the recent status of peregrines in European countries. Spain appears to have the only remaining intact population. He applauds the recovery effort through captive breeding in North America, suggests the technique might restore European peregrines, but points to the loophole it provides in Britain by sheltering wild eggs taken illegally.

There are exceedingly few apparent errors or misinterpretations in the book. It is Townsend's ground squirrel (*Spermophilus townsendii*), not Richardson's ground squirrel (*S. richardsonii*), that figures so importantly into the diet of the raptors of the Snake River Birds of Prey Area in Idaho. The author attributes the habit of feeding exclusively on small alcids in the Queen Charlotte Islands as a unique subspecies specialization of the Peale's Falcon (*F. p. pealei*). He overlooked the fact that about one-third of prey taken by that race in the Aleutians are not alcids. Even in coastal Scotland peregrines catch what is handy; puffins (*Fratercula arctica*) are much the favored prey there. A chap by the name of Tom Speedy reported to Ratcliffe that one coastal eyrie was "a perfect holocaust of Puffins."

The author admits that very few artists catch the real essence of the peregrine. Some of the paintings in this book are stylized and reminiscent of the work of Allan Brooks. Some are especially nice, among these the black-and-white washes that are scattered in the text. The photographs are superb.

The last chapter, entitled "Conservation and the future" falls short of what I feel the author might have said at a time when peregrines in all but a few places in the world are threatened. Is it not appropriate that people such as Ratcliffe, who understand the bird best, give clear recommendations on the course conservation efforts must take? He might have used his careful objectivity to explore the usefulness of recovery strategies and to balance the uses of peregrines by people against the necessity of assuring stable wild populations. Even after the recovery in Britain it is difficult for people to enjoy the bird because of regulations and surveillance.

In the preface, ten or so of the major European and North American works on peregrines are briefly reviewed. This book surely ranks among the better of these in terms of scope, information content and readability.—James H. Enderson.

A Naturalist on a Tropical Farm. By Alexander F. Skutch. Illus. by Dana Gardner. Univ. California Press, Berkeley, California, 1980:405 pp., many line drawings. $16.95.—Of 23 chapters in this book, six are concerned primarily with particular species of wild birds, two with wild mammals and two with insects. Much of the book concerns plants, and all of it concerns the interesting experiences of an observer unique in the depth and breadth of his interests and biological knowledge. In addition to the chapters on particular species (Bicolored antbird [*Gymnopithys bicolor*], Hermit Hummingbird, Speckled Tanager [*Tangara guttata*], Golden-naped Woodpecker [*Melanerpes chrysauchen*], Gray-necked Wood Rail [*Aramides cajanea*] and White-whiskered Softwing [*Malacoptila panamensis*]), virtually every chapter contains interesting observations on birds, espeically on bird-plant relationships, as well as data on migrants and winter birds from temperate breeding grounds, as well as tropical species. The data on the Bicolored Antbird is largely the same as in Skutch (1969 Pacific Coast Avifauna 35). As the author acknowledges, six of the chapters were published earlier elsewhere, but are not all readily available now.

It seems ironic that Skutch has better data on certain aspects of the life history (e.g., duration of parental care after nesting, specific food of young and adult birds) for some tropical species than American ornithologists have been able to acquire over the years for

many temperate zone breeders. Conservation being what it is in much of tropical America, we should be glad that Skutch was there to make the observations. This book, however, is not intended as a technical reference. It is to be read for enjoyment, and the author's writing style seems generally cheerful. The line drawings by Dana Gardner are pleasing and add greatly to the reader's perception of the places and animals discussed.

Anyone planning to visit Central America could profit from the book, and should pay special attention to Chapter 2 on the patterns of weather, the phenology of a tropical year.

First and last, the book is a statement of philosophy from a sensitive man in a world that seems bent on destruction. All of us wish for a world without suffering, but recognize the futility of the wish. Skutch perhaps has thought about it more than most. The summary of his views in the final chapter of the book is worth reading and thinking about, but it is like wishing that the earth was another planet.—Richard R. Graber.

Handbook of the Birds of India and Pakistan. Vol. 2, 2nd ed. By Sálim Ali and S. Dillon Ripley. Oxford University Press, London (England) and New York (New York), 1980:347 pp., 13 color plates, numerous drawings and maps. $34.00.—This is the second of the ten-volume series on birds of the Indian subcontinent to be reprinted. A few small changes have been made in the text and three color plates have been replaced, but otherwise this is the same book first published in 1969. This volume covers the orders Galliformes, Gruiformes and Charadriiformes. Each species is described concisely in a standard format including English, scientific and local names, size, field characters, status, distribution and habitat, general habits, food, voice and calls, breeding, and museum diagnosis. In addition, keys and distribution maps are provided for some groups. As in Volume 1, recently reprinted, this book is printed on cheap paper. This no doubt keeps the price down, but how long will it last?—Robert J. Raikow.

Finding Birds Around the World. By Peter Alden and John Gooders. Houghton Mifflin Co., Boston, Massachusetts, 1981:683 pp., numerous maps. $17.95.—Two widely-traveled observers provide a guide to 111 of the best and most accessible places to see birds around the world. For each area there is a description, information useful to travellers, a map and a checklist. The index lists the birds so that you can find out where to go to see the species you are after. Now all we need is a guide to financing worldwide birding trips. The royalties from books like this?—R.J.R.

Chimney Swifts and Their Relatives. By Margaret Whittemore. Nature Books Publishers, Jackson, Mississippi, 1981:169 pp., numerous drawings and black-and-white photographs, paper cover. $5.95.—A long-time observer's anecdotes and musings on the life of swifts. The photographs are mostly blurred or muddy.—R.J.R.

The "Mid-South Bird Notes" of Ben B. Coffey, Jr. By Jerome A. Jackson (ed.). Special Publication No. 1, Mississippi Ornithological Society, 1981:127 pp., paper cover. Order from Mississippi Ornithological Society, % Dept. of Biological Sciences, Box Z, Mississippi State, Mississippi 39762. $10.00.—This is a compilation of bird records collected and privately published by Coffey from 1952–1956, when there were no state ornithological societies in Arkansas or Mississippi.—R.J.R.

Water and Shore Birds. By Walther Thiede. Chatto & Windus, London, United Kingdom. Distributed in the U.S. by Merrimack Book Service, 99 Main St., Salem, New Hampshire 03078, 1981:143 pp., approx. 128 color plates, paper cover. $5.95.—Intended as a field guide to the commoner shore and water birds of Europe, this book includes accounts of about 117 species of loons, grebes, Fulmar, Gannet, cormorants, herons, storks, ducks, geese, swans, rails, waders, gulls, terns and auks. Its value to American readers will lie in the excellent set of color photographs of the species taken in their natural surroundings.—R.J.R.

Pheasants in Asia 1979. By Christopher Savage (ed.). The World Pheasant Association, 1 Harraton Square, Church Lane, Exning, Suffolk CB8 7HA, United Kingdom, 1980:116 pp., numerous black-and-white illustrations. £8.50.—This paperback book contains the proceedings of the First International Symposium on Pheasants in Asia, held in Nepal in November of 1979. It includes some 29 papers and other reports on the status of pheasants in Asia, field study techniques, captive breeding of pheasants and conservation management.—R.J.R.

Birds of Regina. Revised Edition. By Margaret Belcher, illus. by Fred W. Lahrman. Special Publication No. 12, Saskatchewan Natural History Society, Regina, Saskatchewan, Canada, 1980:151 pp., numerous black-and-white photos and drawings, paper cover. $5.00 + $0.50 postage.—Records of the occurrence, abundance and breeding density of birds in the City of Regina and the surrounding farmlands in a 48 km (30 mile) radius.

Birds of the Qu'Appelle, 1857–1979. By E. Manley Callin. Special Publication No. 13, Saskatchewan Natural History Society, Regina, Saskatchewan, Canada, 1980:168 pp., 4 maps, 10 black-and-white habitat photos, paper cover. $7.00 + $0.50 postage.—An annotated list of bird records from the Qu'Appelle River Valley east of the City of Regina, Saskatchewan.

Nature Saskatoon: An Account of the Saskatoon Natural History Society, 1955–1980. By C. Stuart Houston. Saskatoon Natural History Society, Saskatoon, Saskatchewan, Canada, 1980:46 pp., 7 black-and-white photos, paper cover. $2.50 + $0.50 postage.

These three books may be ordered by mail from the Blue Jay Bookshop, Box 1121, Regina, Saskatchewan S4P 3B4 Canada.—Robert J. Raikow.

Avian Mortality at Man-Made Structures: An Annotated Bibliography (Revised). By Michael L. Avery, Paul F. Springer and Nancy S. Dailey. U.S. Fish and Wildlife Service, Biological Services Program, National Power Plant Team, FWS/OBS-80/54, 1980:152 pp. $5.50.—Revision of FWS/OBS-78/55 (1978). Includes 1042 references, of which 189 are new. Available from the Superintendent of Documents, Washington, D.C., as Stock No. 024-010-00560-2.—R.J.R.

Erratum.—Vol. 93, No. 2, "Cowbird parasitism and evolution of anti-parasite strategies in the Yellow Warbler" by Karen L. Clark and Raleigh J. Robertson. Table 4, p. 253, sub-headings of "Frequency of response" should read "buried," "deserted" and "accepted."—KC

Curtis S. Adkisson, Secretary

The Sixty-second Annual Meeting of the The Wilson Ornithological Society was held Thursday, 4 June to Sunday, 7 June, 1981, at Mount Allison University, Sackville, New Brunswick. The hosts for the meeting were: Canadian Wildlife Service, Atlantic Region; Mount Allison University; and the Chignecto Naturalists' Club. Dr. Anthony J. Erskine chaired the local arrangements committee. One hundred nine persons attended the meeting.

The meeting opened with registration Thursday evening followed by a wine and cheese reception in Hessler Hall of the university. On Friday morning the society was welcomed by Dr. C. W. J. Elliot, Acting Academic Vice President of Mount Allison University. President Geroge A. Hall responded for the society. After the first business meeting, the paper sessions began.

The annual banquet was held in Jennings Hall on Saturday night. Dr. R. G. B. Brown of the Canadian Wildlife Service was the banquet speaker. His talk, summarizing the state of the art in seabird research in eastern Canada, was illustrated by many excellent slides.

At the banquet, President-elect Abbot S. Gaunt announced the following awards:

EDWARDS PRIZES (for best papers appearing in The Wilson Bulletin in 1980)

1) First Edwards Prize to M. Ross Lein, "Display behavior of Ovenbirds (Seiurus aurocapillus): 1. Non-song vocalizations" (Wilson Bulletin 92:312-329).

2) Second Edwards Prize to James F. Wittenberger, "Feeding of secondary nestlings by polygynous male Bobolinks in Oregon" (Wilson Bulletin 92:330-340).

MARGARET MORSE NICE AWARD

Linda Heald, "Behavioral plasticity in a tyrannid flycatcher: effects of environmental variability"

LOUIS AGASSIZ FUERTES GRANT

Mark K. Wourms, "Avian predator discrimination of prey flight patterns"

PAUL A. STEWART AWARDS

Kenneth F. Abraham, "Winter distribution of eastern Arctic Brant geese and the role of the family in locality-use traditions"

David E. Blockstein, "Reproductive behavior and parental investment in the Mourning Dove (Zenaida macroura)"

Roger L. Boyd, "Population movements of Snowy Plovers"

Shari Hahn, "Parent-offspring recognition in Cliff Swallows"

Katherine J. Kuletz, "Breeding success in relation to foraging patterns of Pigeon Guillemots (Cepphus columba), on Naked Island, Prince William Sound, Alaska"

Thomas E. Martin, "Migrants and the dynamics of the bird community of a neotropical second-growth woodland"

Virginia M. Vitt, "The functional basis of roosting behavior in the Common Grackle (Quiscalus quiscula)"

Joseph M. Wunderle, "Uncertainty and the foraging behavior of bananaquits on artificial flowers"

ALEXANDER WILSON PRIZE (for the best student paper at this meeting)

H. Carolyn Peach, "The foraging ecology of adult and juvenile Semipalmated Plover (Charadrius semipalmatus Bonaparte) on the Starrs Point Mudflat, Minas Basin, Bay of Fundy"

There were field trips to Amherst Point Bird Sanctuary and Ram Pasture Salt Marsh. On Sunday there was an excursion to the Upper Bay of Fundy shore. On Sunday there were all-day trips to Cape Tryon, Prince Edward Island, and Fundy National Park, New Brunswick.

FIRST BUSINESS MEETING

The first business meeting, held on 5 June 1981, was presided over by President George A. Hall. He announced the posting of the list of new members, and appointed the Alexander Wilson Prize Committee, consisting of Keith Bildstein, George Kulesza, and James Rising, and the Auditing Committee, consisting of William Klamm and Hubert Zernichow. He also announced that anyone interested in submitting resolutions to be published as part of this meeting should contact Helen Lapham or Kathleen Anderson of the Resolutions Committee. Secretary Curtis S. Adkisson summarized actions taken at the 1981 meeting of the Council, held on Thursday, 4 June. Jon C. Barlow was re-elected Editor of The Wilson Bulletin. It is the Council's intent to have a list of the holdings of the Van Tyne Memorial Library as well as the recommendations of the Conservation Committee published in The Wilson Bulletin in the near future. Council recognizes that planning should begin soon for the Wilson Ornithological Society centennial in 1988. President Hall then presided over the passage by voice vote of an amendment to the Bylaws (see Wilson Bulletin 92:465) such that membership applications be sent to the Treasurer instead of to the Secretary.

The final item of business at this meeting was the Treasurer's Report, by Robert D. Burns.

REPORT OF THE TREASURER
1 JANUARY 1980 TO 31 DECEMBER 1980
GENERAL FUNDS

RECEIPTS		
Student and Regular Membership Dues Collected in 1980		
For 1980	$10,779.58	
For 1981	15,284.50	
Family Memberships for 1981	292.00	
Sustaining Membership for 1981	1,462.00	
TOTAL DUES		$27,818.08
Subscriptions to THE WILSON BULLETIN		
For 1980	6,181.00	
For 1981	5,477.50	
TOTAL SUBSCRIPTIONS		11,658.50
Back Issues of THE WILSON BULLETIN		338.50
Interest and Dividends		12,719.78
Royalties		808.63
Contributtions from Authors		2,339.17
Contributions to Special President's Fund		100.00
Contributions to the General Fund		445.00
Contributions and Life Memberships to Endowment		2,864.50
TOTAL RECEIPTS - Jan. 1, 1980 to Dec. 31, 1980		$59,092.16
DISBURSEMENTS		
WILSON BULLETIN		
December	$ 8,983.59	
March	8,874.10	
June	9,005.82	
September	8,969.40	
Colorplates	3,366.20	
Insurance	23.00	
Reprint Back Issues	1,543.52	
TOTAL WILSON BULLETIN PRODUCTION COSTS		$40,765.63
Additions to Endowment Trust at Central Counties Bank		1,700.00
Endowment Funds Transferred to Stewart Fund		800.00
Endowment Funds Transferred to Wilson Prize		100.00
Dues to International Council for Bird Preservation 1979 & 1980		200.00

DISBURSEMENTS (continued)

Editor's Expenses		$ 479.00
Treasurer's Expenses (200 stamps)		30.00
Secretary's Expenses (stationery)		36.05
Ornithological Societies of North America	$9,678.72	
Grant from ARCO plus AOU Refund	(1,854.63)	7,824.09
TOTAL DISBURSEMENTS - Jan. 1, 1980 to Dec. 31, 1980		$51,934.77

CASH ACCOUNTS

Checking Account, 31 December 1980	$ 9,210.55	
Savings Account, 31 December 1980	16,644.65	
Total Cash on Hand		$25,855.20

DESIGNATED ACCOUNTS

VAN TYNE MEMORIAL LIBRARY FUND

RECEIPTS		
Balance 1979	$ 1,283.39	
Sales and Gifts	679.59	
DISBURSEMENTS		
Purchase of Books	788.40	
Balance		$ 1,174.58

LOUIS AGASSIZ FUERTES RESEARCH FUND

RECEIPTS	
Gifts	200.00
DISBURSEMENTS	
Gregory S. Butcher	200.00

MARGARET MORSE NICE FUND

RECEIPTS	
Gift	100.00
DISBURSEMENTS	
Nancy Newfield	100.00

ALEXANDER WILSON PRIZE

RECEIPTS	
From Endowment	100.00
DISBURSEMENTS	
M. W. Collopy and K. Collopy	100.00

ERNEST P. EDWARDS PRIZE

RECEIPTS	
E. P. Edwards	$ 350.00
DISBURSEMENTS	
Ellen D. Ketterson	225.00
Charles R. Brown	125.00

PAUL A. STEWART AWARDS

RECEIPTS	
From Endowment	800.00
DISBURSEMENTS	
Gregory A. Perkins	200.00
Scott. R. Winterstein	200.00
Bruce B. Edinger	200.00
Diane E. Riska	200.00

AARON BAGG STUDENT MEMBERSHIP AWARD FUND

RECEIPTS		
Balance from 1979	30.00	
Gift	200.00	
DISBURSEMENTS		
20 Student Awards	200.00	
Balance		$ 30.00

ENDOWMENT

RECEIPTS		
Value of General Endowment Fund Dec. 31, 1979	132,812.78	
Life Membership Payments and Gifts	2,864.54	
Appreciation on Principle	2,174.72	
Value of General Endowment Fund Dec. 31, 1980		$137,852.04

GEORGE M. SUTTON COLORPLATE FUND

Value	27,121.25
Total combined Wilson Ornithological Society Endowment Funds December 31, 1980	164,973.29
Earnings from Endowment for 1980	12,719.78
Rate of return for 1980 7.71%	

SECOND BUSINESS MEETING

The second business meeting was convened by President Hall on Saturday afternoon, 6 June 1981. The proposed new members were elected unanimously. Hubert Zernichow presented the Auditors' Report, which was accepted by the membership. Four resolutions presented by the Resolutions Committee, after some debate and amendment, were approved. These, and summaries of committee reports presented at the meeting of Council, are included below.

AUDITING COMMITTEE REPORT - 1980

We, the undersigned, have examined the Treasurer's records, bank statements, certificate of deposit, cancelled checks, and other financial records of the Society covering the period 1 January 1980 to 31 December 1980.

Our examination confirms that receipts and disbursements have been correctly accounted for, and bank balances are in agreement with the Treasurer's statement.

Hubert P. Zernichow, member
William A. Klamm, member

EDITOR'S REPORT - 1980

The Wilson Bulletin editorial staff processed 330 manuscripts in 1980, including 150 received as new in that year. The higher quality of papers submitted is reflected in a 10.4% decrease in rejection rate. Volume 92 contained 33 major articles, and 49 notes, for a total of 564 pages.

There is good material on hand for color plates for the next several issues. In addition, access has been granted to several previously unpublished paintings of the late L. A. Fuertes.

I have geen greatly helped by people in the editorial office and elsewhere, including K. C. Parkes, Keith Bildstein, and David Ankney (editorial assistants), John O'Neill, George Miksch Sutton, William Lunk, Sandra Gaunt, A. S. Gaunt, George Hall, Peter Stettenheim, and Guy Dresser and Ken Blair (both of Allen Press). I continue to enjoy working with The Wilson Bulletin and will be pleased to continue as Editor.

Jon C. Barlow, Editor

LIBRARY COMMITTEE REPORT - 1980

The Josselyn Van Tyne Memorial Library continued to run smoothly during the 1980 calendar year. As in the preceding year, 149 journals and newsletters were received through 115 exchanges; there were 35 gifts and complimentary subscriptions, plus 2 regular subscriptions. This adds up to 186 titles. Col. L. R. Wolfe deserves our special thanks for his regular donation of Raptor Research and of other journal issues.

Work on the translation file goes on; this adjunct to our library should more and more help workers to at least some insight into foreign publications in the field. Sales of duplicates during the year brought in $263.00 to our New Book Fund; $460 was spent from the fund, to purchase 49 new books and journals deemed to be critically needed. Contributions of cash, as well as of duplicates for sale, would always be most welcome.

Loans to 61 members involved 380 items and 97 separate shipments. This, it must be understood, is in addition to the constant on-the-spot usage the collection receives. Member participation is still the essential basis of the library's growth: 2175 items by 26 members; 46 books, 1380 reprints, 347 reports and pamphlets, 272 journal issues, 16 translations, 76 maps, and 4 theses.

Donors recorded were W. and D. Behling, A. J. Berger (again, 1035 items, or nearly half the total!), C. R. Brown, F. Hamerstrom, H. Harrison, C. J. Henny, J. Hinshaw, T. H. Hubbell, A. S. Hyde, P. Johnsgard, L. Kelso, F. E. Lohrer, H. Mayfield, R. B. Payne, B. Pinkowski, S. Postupalsky, K. Prescott, W. J. Richardson, D. Siegel-Causey, A. Simon, R. W. Storer, J. Strauch, Jr., J. Tate, Jr., S. Wilbur, J. E. Willoughby, and Col. L. R. Wolfe.

As always, the committee thanks the entire membership, urging your continued and increased support in the years to come.

William R. Lunk, Chairman

MEMBERSHIP COMMITTEE REPORT - 1980

Total paid membership for the Society was 2,162 in calendar year 1980. The figure for 1981 is 2,257 (a net increase of 95 or 4.4%). My office has handled a total of 53 requests for membership applications since the last meeting, as well as about 20 actual payments. Requests for applications were usually handled on the same day, while payments were forwarded to OSNA in Columbus, Ohio. To increase membership the Society should have new folders printed, and these can be sent, along with a letter of invitation, to members of other ornithological societies who are not Wilson members.

Robert C. Whitmore, Chairman

STUDENT MEMBERSHIP COMMITTEE REPORT - 1980

Announcement of the Aaron M. Bagg Student Membership Awards was made in The Wilson Bulletin and Ornithological Newsletter. An announcement was also sent to 205 members of the Society along with application materials for the Bagg Award. Application materials were also sent in response to 21 letters of inquiry. There were 46 eligible applicants for the Bagg Award, an increase of 92% over last year. Funds for 16 awards were available. The student

awardees and their institutions are as follows: Douglas A. Bell, Westfalische Wilhelms-Univ., Munster, West Germany; Thomas Bicak, University of Montana; Scott P. Carroll, University of Oklahoma; Dominick A. Della Sala, Wayne State University; Sylvia L. Halkin, University of Oklahoma; Elizabeth G. Henderson, University of South Carolina; William J. Hilton, Jr., University of Minnesota; Mark L. Hoffman, University of Florida; Charles T. LaRue, Northern Arizona University; David M. Lyons, Frostburg State College; Kelvin G. Murray, University of Florida; James S. Quinn, University of Oklahoma; Roland L. Redmond, University of Montana; David E. Seibel, University of Kansas, David A. Spector, Stockton State College; Kathy A. Winnett-Murray, University of Florida.

Nominations for student membership were received for 18 students. These nominees, as well as the 30 unsuccessful Bagg Award applicants were sent a letter of invitation to join the Society. These students also received a letter from Kathy Groschupf (VPI&SU, Blacksburg) and her ad hoc committee for student membership composed of Bette Schardien (Mississippi State) and Susan Dohlert (West Virginia University). This committee also sent a letter outlining the benefits of student membership to 100 graduate departments.

This committee's work would be greatly aided by an increase in WOS membership participation in the process of nominating both potential Bagg Awardees and regular student members.

John L. Zimmerman, Chairman
Thomas C. Grubb
Roland R. Roth
Charles F. Leck

REPORT OF THE RESOLUTIONS COMMITTEE

The following resolutions were read and passed at the second business meeting:

WHEREAS the continental shelf of Newfoundland, Nova Scotia, and New England supports seabirds from broad areas as far apart as the Arctic Ocean of Europe and North America and the South Atlantic Ocean, as well as providing renewable fisheries resources of critical importance to human populations, and,

WHEREAS the exploration, development, and transportation of hydrocarbon resources in the offshore areas are imminent, and,

WHEREAS the environmental impact of such activities, especially when resulting in oil spills, poses a serious threat to marine life, especially birds:

THEREFORE BE IT RESOLVED that the Wilson Ornithological Society asks the Canadian and United States governments to proceed with utmost caution in licensing all aspects of such operations and to ensure that the protection of the marine

environment be a fundamental consideration at every stage of the decision-making process.

WHEREAS the barrier islands and their associated habitats of the United States have unique natural, ecological and biological values important to wildlife and a human population, and,
WHEREAS these values have been recognized in the Department of the Interior's 1979 "Barrier Island Protection Plan" under which the Fish and Wildlife Service has identified some fifty barrier islands along the Atlantic and Gulf coasts with exceptional fish and wildlife values, and,
WHEREAS nearly twenty federal agencies presently have programs affecting these areas of which three-quarters foster adverse effects through grants, loans, insurance and disaster-relief programs with subsidized development, and,
WHEREAS the present administration emphasizes the need to reduce federal spending:
THEREFORE BE IT RESOLVED that the Wilson Ornithological Society supports pending bills H.R. 3252 and S. 1018 which seek to establish a barrier island protection system to perpetuate wildlife resources and which cut off the subsidies encouraging development, and,
FURTHERMORE BE IT RESOLVED that the Society requests the administration to provide a coordinated, consistent policy among its agencies to preserve this fragile, valuable habitat.

WHEREAS Ronald Reagan while governor of California showed commendable concern for environmental problems, and built a fine record of achievement in conservation legislation and executive action, and,
WHEREAS since he became President of the United States he has devoted most of his energies toward solving the current economic and defense problems, and has been further hampered in his attention to other vital concerns by the senseless and lamentable attempt on his life, and has allowed many of his appointees to operate on their personal biases, which so not reflect the wishes of the great majority of the American people, and,
WHEREAS national surveys have shown that the majority of American citizens realize the environment is a complex and fragile natural system and must be protected from unwarranted destruction and degradation - a concern clearly reflected by Mr. Reagan's past actions, and,
WHEREAS the members of the Wilson Ornithological Society, part of the concerned majority, believe the future of humankind on this planet is in the hands of the present generation:

THEREFORE BE IT RESOLVED the Wilson Ornithological Society requests that President Reagan exert closer supervision of his appointees in environmental agencies:
FURTHERMORE BE IT RESOLVED the Wilson Ornithological Society encourages its members to inform their congressional representatives and the executive branch that astute environmental legislation provides long-term solutions to continuing problems and should not be sacrificed to short-term palliatives for momentary crises.

WHEREAS The Canadian Wildlife Service, Mount Allison University, and the Chignecto Naturalists' Club have hosted the 1981 Wilson Ornithological Society meeting in Sackville, New Brunswick, June fourth through eighth, and,
WHEREAS the meetings have been conducted smoothly and with hospitality on the beautiful Mount Allison campus, and,
WHEREAS the birding trips, the three offered Friday and Saturday mornings and the two full-day trips, as well as the especially enjoyable spouses' trips to historical sites, have covered different habitats and birds, introducing this beautiful countryside and its varied birdlife to Wilson members, and,
WHEREAS the lobster boil sponsored by the government of the province of New Brunswick was a delicious treat for gourmet and non-gourmet alike:
THEREFORE BE IT RESOLVED that the Wilson Ornithological Society gives its grateful thanks to these organizations and especially to Anthony Erskine and the rest of the local committee for the success and enjoyment of the meeting.

NOMINATING COMMITTEE REPORT - 1980

As the final item of business the Nominating Committee of Kathleen S. Anderson, Jerome A. Jackson, and Kenneth C. Parkes, chairman, submitted the following slate of officers for 1981-82: President, Abbot S. Gaunt; First Vice-President, Jerome A. Jackson; Second Vice-President, Clait E. Braun; Secretary, Curtis S. Adkisson; Treasurer, Robert D. Burns; Council Member for three-year term beginning at the end of the 1981 meeting, Helen S. Lapham. There being no further nominations, it was moved, seconded and passed that the Secretary be instructed to cast a unanimous ballot for the slate.

PAPERS SESSION

The papers session was organized by Jerome A. Jackson. Individual parts of the session were chaired by: Kathleen Anderson, Jon Barlow, Clait Braun, A. S. Gaunt, Jerome Jackson, George Kulesza, Helmut Mueller, and Richard Stiehl. A list of papers presented follows:

R. E. Simmons, Acadia University, "Polygyny and breeding success in the Northern Harrier, - violation of a model?"

Keith L. Bildstein, Winthrop College, "Small males and large females: causes and consequences in Northern Harriers"

Norman R. Seymour, St. Francis Xavier University, and Robert Bancroft, Nova Scotia Department of Lands and Forests, "Use of two habitats by Ospreys (Pandion haliaetus) related to changes in prey availability"

Paul Kerlinger, SUNY, Albany, "Water crossing behavior by raptors during migration"

Maurice N. Lefranc, Jr, and William S. Clark, Raptor Information Center, National Wildlife Federation, "Variability of wing loading in North American birds of prey"

Elizabeth Henderson, University of South Carolina and Belle Baruch Inst., "Feeding behavior of adult White Ibis on a South Carolina salt marsh. 1. Habitat effects"

Richard B. Stiehl, University of Wisconsin-Green Bay, "Food habits of nestling Common Ravens"

P. O. Dunn, M. A. McCollough, and T. A. May, University of Maine-Orono, "Length of stay and fat reserves of Semipalmated Sandpipers in eastern Maine"

Jonas Hedberg and T. A. May, University of Maine-Orono, "Habitat selection by Spruce Grouse in eastern Maine"

Clait E. Braun and Kenneth M. Giesen, Colorado Division of Wildlife, "Survival of female White-tailed Ptarmigan in Colorado"

James A. Mosher and Kimberly Titus, University of Maryland-Frostburg, "Principal components analysis of nest site selection by the Broad-winged Hawk (Buteo platypterus)"

Bette J. Schardien, Mississippi State University, "Resident status and nesting phenology of Killdeer in Mississippi"

Rhett Talbert, media specialist, and presented by Keith Bildstein, Belle Baruch Institute, University of South Carolina, "Opportunities for behavioral and ornithological research at Hobcaw Barony"

James A. Mosher and Kimberly Titus, University of Maryland-Frostburg, "A chance corrective classification procedure for use in discriminant analysis"

Maurice N. Lefranc, Jr., National Wildlife Federation, " The National Wildlife Federation's Raptor Information Center"

Robert J. O'Hara, University of Massachusetts, "The evolution of longspurs (Emberizidae)"

J. D. Rising, University of Toronto, "Tests of hypotheses about the evolution

of sexual dimorphism in birds"

S. L. Berman, College of the Holy Cross, "Hind limb myology of the Mousebirds"

Jay Pitocchelli, Memorial University of Newfoundland, "Song dialects, and vocal development in Savannah Sparrows (Passerculus sandwichensis labradorius) in Newfoundland and the St. Pierre et Miguelon Islands"

Charles P. Nicholson, Tennessee Valley Authority, "Song variation in the Swainson's Warbler"

Daniel S. McGeen, Pontiac, Michigan, "Kirtland's Warbler, endangered or doomed"

George Kulesza, Mississippi State University,"Life history correlations among passerine birds"

Charles G. Sibley and Jon Ahlquist, Yale University, "The relationships of the vireos (Vireonidae) as indicated by DNA-DNA hybridization"

Ann Greene and David N. Nettleship, Canadian Wildlife Service, "Attendance patterns of Northern Fulmars at Prince Leopold Island"

Howard R. Postovit, North Dakota State University, James Tate, Jr., ARCO Coal Co., and James W. Grier, North Dakota State University, "A new nest platform for tree-nesting eagles"

C. S. Adkisson, Virginia Polytechnic Inst. and State University, "An ethological comparison of European Bullfinches and Pine Grosbeaks"

Jerome A. Jackson, Mississippi State University, "Home range and habitat use of Red-cockaded Woodpeckers in 'poor' habitat"

Norman C. Famous, Machias, Maine, and Stewart I. Fefer, U. S. Fish and Wildlife Service, "Migratory shorebird assessment in eastern Maine"

H. Carolyn Peach, Acadia University, "The foraging ecology of adult and juvenile Semipalmated Plover (Charadrius semipalmatus Bonaparte) on the Starrs Point Mudflat, Minas Basin, Bay of Fundy"

Kevin J. Cash, Acadia University, "Food remains of the Northern Bald Eagle (Haliaeetus leucocephalus alascanus Townsend) in summer at nest sites on Cape Breton Island, Nova Scotia"

Peter R. N. MacDonald, Acadia University, "Age-related foraging behaviour of the Northern Bald Eagle (Haliaeetus leucocephalus alascanus Townsend) at a wintering site in Nova Scotia.

ATTENDANCE

BRITISH COLUMBIA: Burnaby, Wayne Weber.

NEW BRUNSWICK: Albert, David Christi, Mary Majka; Memramcook, Reid McManus, Mary O'Rourke; Sackville, Paul Bogaard, Kevin Cash, Tony Erskine, Gay Hansen, Peter Hicklin, Bob Lamberton, Lance Laviolette, Mag MacInnis,

H. Carolyn Peach, Al Smith, Stuart Tingley.

NEWFOUNDLAND: Glovertown, Roger T. Burrows; Portugal Cove, Margaret Purdy; St. John's, Christine Paton, Jay Pitochelli.

NOVA SCOTIA: Antigonish, Norman Seymour; Dartmouth, Dick Brown; Elmsdale, Andrew MacInnis; Gaspman, Cyril Coldwell; Halifax, Earle Hickey, Tony Lock; Kentville, Peter Austin-Smith, Mark Forbes; Wolfville, Phoebe Barnard, Carolyn Crawford, Andree Dubois, Peter MacDonald, Patricia Reid, Bob Simmons, P. C. Smith.

ONTARIO: Gore's Landing, Norman D. Martin; Toronto, Jon C. Barlow, Margaret May, Thomas Parsons, John Reynolds, James D. Rising.

PRINCE EDWARD ISLAND: Bloomfield, Alanagh MacDougall, Gerald MacDougall.

QUEBEC: Senneville, Margaret Elliot.

COLORADO: Fort Collins, Clait E. Braun; Golden, James Tate, Jr.

CONNECTICUT: New Canaan, Elise Lapham; New Haven, Charles G. Sibley.

DISTRICT OF COLUMBIA: Washington, Earl Baysinger.

FLORIDA: Gainesville, Mary H. Clench; Winter Park, Fred H. Glenny.

IOWA: Sioux City, Morgan Webb.

KENTUCKY: Richmond, Gary Ritchison.

MAINE: Brunswick, Charles Huntington; Orono, Thomas A. Allen, Norm Famous, Mark McCollough, Terry May; Tenant's Harbor, Ralph S. Palmer.

MARYLAND: Frostburg, James Mosher.

MASSACHUSETTS: Amherst, Robert O'Hara; Lincoln, Peter Alden; Manomet, Kathleen Anderson, Michael Chick, Trevor Lloyd-Evans; Petersham, John and Rosalie Fiske; Worcester, Susan L. Berman.

MICHIGAN: Alma, Alma and Lester Eyer; Grass Lake, Harold Ratcliff; Jackson, Robert A. Whiting; Pleasant Lake, Hubert P. Zernichow; Pontiac, Daniel McGeen.

MINNESOTA: Duluth, Pershing B. Hofslund.

MISSISSIPPI: Mississippi State, Opal Dakin, Jerome Jackson, George Kulesza, Bette J. Schardien.

NEW JERSEY: Trenton, Mary E. Doscher.

NEW YORK: Albany, Paul Kerlinger; Lansing, Helen Lapham; Phoenix, Vincent J. Lucid.

NORTH CAROLINA: Chapel Hill, Helmut Meuller, Nancy Mueller.

OHIO: Columbus, Abbot Gaunt, Sandra Gaunt; Gambier, Robert D. Burns; Lakewood, Willaim Klamm, Mrs. William Klamm; Painesville, Mrs. Robert Booth.

OKLAHOMA: Edmond, Christine Albasi, W. J. Radke.

PENNSYLVANIA: Chester Springs, Phillips B. Street; Pittsburgh, Jay Loughlin.

SOUTH CAROLINA: Chester, Mrs. W. S. Robinson, Mrs. W. S. Stone, Sr.; Columbia, Elizabeth Henderson, Rock Hill, Keith Bildstein; Spartanburg, Miller C. Foster, Jr.

TENNESSEE: Knoxville, Marcia Davis, Beth Lacy; Maryville, Ralph. J. Zaenglein; Norris, Charles P. Nicholson, Linda J. Turner.

TEXAS: Austin, Charles Hartshorne.

VIRGINIA: Blacksburg, C. S. Adkisson; Bluemont, Maurice Lefranc.

WEST VIRGINIA: Morgantown, George A. Hall.

WISCONSIN: New Franklin, Richard Stiehl.

The next Annual Meeting of the society will be held at Virginia Polytechnic Institute and State University in Blacksburg, Virginia, from 6 to 9 May 1982. In addition to a scientific program, an art exhibit, and a program for spouses, there will be field trips into the mountains around Blacksburg where many bird species characteristic of northern hardwood and coniferous forests will already be in residence.

INDEX TO VOLUME 93, 1981

By Nancy J. Flood, Janet T. Mannone and Gary R. Bortolotti

This index includes references to genera, species, authors and key words or terms. In addition to avian species, references are made to the scientific names of all vertebrates mentioned within the volume. Common names are as they appeared in the volume. Reference is made to books reviewed, reviewers and announcements as they appeared in the volume.

abnormality
  of bill of Agelaius phoeniceus, 563–565
Abraham, Kenneth F., Pierre Mineau and Fred Cooke, Re-mating of a Lesser Snow Goose, 557–559
Accipiter cooperii, 110
  nisus, 89, 286
  striatus, 85–92, 491–499
Acrocephalus palustris, 59
  scirpaceus, 59
Actitis macularia, 328
Aechmophorus occidentalis, 330
aerodynamics
  advantages of tail keeling in Quiscalus quiscula, 500–505
  age and sex differences in Accipiter striatus, 491–499
Afton, Alan D., see Cooper, James A. and ———
Agapornis spp., 297–298
Agelaius phoeniceus, 119–121, 444, 540, 547–548, 563–565
Ainley, David G., see DeSante, David F. and ———
Aix sponsa, 330–331
Ajaia ajaja, 151, 548
Albatross, Black-browed, see Diomedea melanophris
  Black-footed, see Diomedea nigripes
  Gray-headed, see Diomedea chrysostoma
  Laysan, see Diomedea immutabilis
  Light-mantled Sooty, see Phoebetria palpebrata
  Wandering, see Diomedea exulans
albatross, see Diomedea spp.
Alca torda, 110
Alces alces, 102
Alden, Peter and John Gooders, Finding birds around the world, reviewed, 573
Ali, Sálim and S. Dillon Ripley, Handbook of the birds of India and Pakistan. Vol. 2, 2nd ed., reviewed, 573
Allez, George, see Mueller, Helmut C., Daniel D. Berger and ———
allopatry
  in chickadees, 54–66
Amaurolimnas concolor, 107–108
Amazona, 297
Ammodramus aurifrons, 282
  savannarum, 547–548
Ammospiza caudacuta, 443
  maritima, 443
  maritima nigrescens, 443, 540
Anas acuta, 330, 445
  americana, 274, 330
  clypeata, 330, 445
  crecca carolinensis, 330
  cyanoptera, 403–405
  discors, 330, 403–405
  platyrhynchos, 121–124, 277–278, 440, 562–563
  rubripes, 449
  strepera, 274, 276–277, 330
Anas spp., 289
Anderson, R. M., B. D. Turner and L. R. Taylor (eds.), Population dynamics: the 20th symposium of the British Ecological Society, reviewed, 288–289
Anískowicz, B. T., Behavior of a male Least Bittern incubating after loss of mate, 395–397
announcements
  Association of Systematics Collections Program evaluation, 382
  formation of the International Osprey Foundation, Inc., 333
  formation of the Meandarra Ornithological Field Study Unit, 41

International Commission on Zoological Nomenclature, 41, 349
memorial note, Helen Van Tyne, 135
Anolis sp., 107
Anser anser, 320
caerulescens caerulescens, 121–124, 444, 557–559
Anseriformes, 407–412
Antarctica, 1–20
Antbird, Bicolored, see Gymnopithys bicolor
Black-headed, see Percnostola rufifrons
Narrow-billed, see Formicivora iheringi
Slender, see Rhopornis ardesiaca
Spotted, see Hylophylax naevioides
White-bellied, see Myrmeciza longipes
White-bibbed, see Myrmeciza loricata
ants, 528
army, see Eciton sp.
Anurolimnas castaneiceps, 141
fasciatus, 141
viridis, 141
Aphelocoma coerulescens, 538, 549, 550
ultramarina, 551
Aptenodytes forsteri, 5–20
Apus apus, 79, 82, 550
Aquila chrysaetos, 92, 109
pomarina, 286
verreauxi, 286
Aramides cajanea, 572
Aramides sp., 107, 108
Archibald, G. W., see Nesbitt, Stephen A. and ———
Archilochus alexandri, 405–406
colubris, 218–242
Archoplites interruptus, 556
Ardea cinerea, 145–163
herodias, 145–163
goliatha, 145–163
Ardeola greyii, 550
ralloides, 550
Ardeola spp., 550
Arenaria interpres, 446
Asio flammeus, 330
otus, 110
Auklet, Cassin's, see Ptychoramphus aleuticа
Rhinoceros, see Cerorhinca monocerata
Auriparus flaviceps, 203
Avery, Michael L., Paul F. Springer and Nancy S. Dailey, Avian mortality at man-made structures: an annotated bibliography. Rev., reviewed, 574
awards and grants
Aaron M. Bagg student membership awards, 136, 356
Louis Agassiz Fuertes, Margaret Morse Nice and Paul A. Stewart awards, 356
research grants, 324
Aythya affinis, 330
americana, 330, 445, 562–563
collaris, 330
valisineria, 330, 443, 548
Balda, Russell P., see Szaro, Robert C. and ———
Balgooyen, Thomas G., review by, 423–424
Baker, James L., see Rakestraw, James L. and ———
Baptista, Luis F., Martin L. Morton and Maria E. Pereyra, Interspecific song mimesis by a Lincoln Sparrow, 265–267
Barth, Larry, review by, 295–296
Bartramia longicauda, 547–548
Basileuterus culicivorus, 278
Baumel, J. J., A. S. King, A. M. Lucas, J. E. Breazile and H. E. Evans (eds.), Nomina anatomica avium: an annotated anatomical dictionary of birds, reviewed, 125–126, 126–128
beetles, see Coleoptera
behavior
agonistic
Grus canadensis, 99–103
White-breasted Nuthatches, 271–274
breeding
Anser caerulescens caerulescens, 557–559
copulatory
Sterna maxima, 390–391
courtship
Sterna maxima, 390–391
display
Bonasa umbellus, 98–99
Capella gallinago, 457–461, 472–473 (Frontispiece)
Capella gallinago magellanica, 466–467
Capella gallinago nigripennis, 467–468
Capella gallinago paraguaiae, 465–466
Capella hardwickii, 463

Capella imperialis, 470–471
Capella jamesoni, 470
Capella megala, 463–464
Capella nemoricola, 464
Capella solitaria, 462–463
Capella stenura, 461–462
Capella stricklandii, 470
Capella stricklandii jamesoni, 471
Capella undulata, 471–472
Eremophila alpestris, 522
Grus canadensis, 99–103
Lymnocryptes minimus, 472
Seiurus aurocapillus, 21–41
diversionary
Somateria molissima, 559–560
flight
Buteo jamaicensis, 350–356
food-related
Accipiter striatus, 85–92
Ammospiza maritima nigrescens feeds Agelaius phoeniceus fledglings, 540
Branta canadensis, 310–324
Bubulcus ibis, 549–550
Dendrocygna autumnalis, 551–554
Dendroica coronata, 334–339
Dendroica virens, 334–339, 478–490
Empidonax viriscens, 478–490
Eremophila alpestris, 528–529
Parus atricapillus, 393–394
Passer domesticus, 554
passerines, 391–392
Pelecanus erythrorhynchos, 554–556
Phalacrocorax auritus, 554–556
Phalaropus fulicarius, 557
Piranga olivacea, 478–490
Rhopornis ardesiaca, 103–107
Setophaga ruticilla, 478–490
wading birds, 145–163
incubation
Ixobrychus exilis, 395–397
nesting
system for monitoring, 325–333
parental
Corvus brachyrhynchos, 394–395
play
Coragyps atratus, 97
roosting
Chaetura pelagica, 77–84
sentinel
Corvus brachyrhynchos, 394–395
social
Branta canadensis, 310–324
territorial
Eremophila alpestris, 520–522
Podiceps auritus, 560–561
winter
Haliaeetus leucocephalus, 259–264
Belcher, Margaret, Birds of Regina, Rev. Ed., reviewed, 574
Belitsky, David W., see Schreiber, Ralph W., ——— and Bruce A. Sorrie
Bellrose, Frank C. and R. C. Crompton, Migration speeds of waterfowl species, 121–124
Berger, Andrew J., see Kear, Janet and ———
Berger, Daniel D., see Mueller, Helmut C., ——— and George Allez
Berman, Susan L., reviews by, 296–297, 297–298
Bierly, Michael Lee, Bird finding in Tennessee, reviewed, 300
Bittern, Least, see Ixobrychus exilis
Blackbird, European, see Turdus merula
Red-winged, see Agelaius phoeniceus
Rusty, see Euphagus carolinus
Blackcap, see Sylvia atricapilla
Blohm, Robert J., Additional evidence of egg-moving behavior by female Gadwalls, 276–277
Bluebird, Mountain, see Sialia currucoides
bluefish, see Pomatomus saltatrix
Bolen, Eric G., review by, 133–134
Bombycilla cedrorum, 253
Bonasa umbellus, 98–99, 218–242, 291, 372–382
boobies, see Sula spp.
Bothrops lateralis, 278
Bourne, Godfrey R., Food habits of Black-bellied Whistling Ducks occupying rice culture habitats, 551–554
Boxall, Peter C., see Stepney, Philip H. R. and ———
Brachyramphus brevirostris, 402
marmoratus, 400–403
marmoratus marmoratus, 402
marmoratus perdix, 402
Brant, Black, see Branta bernicla

Branta bernicla, 438, 548
bernicla nigricans, 446
canadensis interior, 121–124, 207–217, 318, 319, 330, 559
canadensis maxima, 310–324
sandvicensis, 417–419
Braun, Clait E., see Gorenzel, Warner P., Ronald A. Ryder and ———
Breazile, J. E., see Baumel, J. J. et al.
breeding biology, general
Eremophila alpestris, 519–530
Icterus gularis, 531–537
Pelecanus occidentalis, 397–400
Petrochelidon fulva, 507–518
breeding success
Columba livia, 357–362
Bubalus bubalis, 550
Bubo virginianus, 110
Bubulcus ibis, 147, 549–550
Bucephala albeola, 443
buffalo, water, see Bubalus bubalis
Bufflehead, see Bucephala albeola
Bufo marinus, 552, 553
bug, Mexican chicken, see Haematosiphon indorus
bullhead, brown, see Ictalurus nebulosus
Bunting, Indigo, see Passerina cyanea
Lazuli, see Passerina amoena
Snow, see Plectrophenax nivalis
Buphagus spp., 549
Burger, Joanna, review by, 131–132
Bush-tanager, Common, see Chlorospingus ophthalmicus
Buskirk, William H., Ochraceous Wren fails to respond to mobbing calls in a heterospecific flock, 278–279
Buteo albonotatus, 282–284
jamaicensis, 110, 350–356
lagopus, 350
lineatus, 110
platypterus, 110
regalis, 92–97, 354
Butorides virescens, 147
Calandra sp., 553
Calidris canutus, 557
Callin, E. Manley, Birds of the Qu'appelle, 1857–1979, reviewed, 574
Calocitta formosa, 539
Campbell, Kenneth E., Jr., Papers in avian paleontology honoring Hildegarde Howard, reviewed, 407–412
Campylorhynchus brunneicapillus, 203
Canachites canadensis, 291, 376
Cannings, Richard J. and William Threlfall, Horned Lark breeding biology at Cape St. Mary's, Newfoundland, 519–530
Canvasback, see Aythya valisineria
Capella gallinago, 457–474 (Frontispiece)
gallinago andina, 465, 467, 469, 474
gallinago angolensis, 465, 468
gallinago delicata, 460, 465, 469
gallinago faeroensis, 460, 465
gallinago gallinago, 460, 465, 474
gallinago magellanica, 465, 466–467
gallinago nigripennis, 465, 467–468
gallinago paraguaiae, 465–466, 472
hardwickii, 463
imperialis, 468, 470–471
jamesoni, 468, 469, 470, 471
macrodactyla, 465, 468–469
media, 459, 462, 467, 474
megala, 460, 463–464
nemoricola, 464
nobilis, 465, 467, 468–470
solitaria, 462–463
stenura, 460, 461–462, 468, 474
stricklandii, 468, 470, 471
stricklandii jamesoni, 471
undulata, 468, 471, 474
Capercaillie, see Tetrao urogallus
Black-billed, see Tetrao parvirostris
Caprimulgis carolinensis, 363–371
vociferus, 363–371
Carcharinus leucas, 279
longimanus, 279
Carcharodon carcharias, 279
Cardinal, see Cardinalis cardinalis
Cardinalis cardinalis, 218–242
Carduelis pinus, 344, 346
carp, see Cyprinus carpio
Carpodacus purpureus, 551
cat, domestic, see Felis domestica
Catbird, Gray, see Dumetella carolinensis
Catharacta maccormicki, 12
Catharacta spp., 443
Catharus frantzii, 302
fuscescens, 218–242
guttata, 164–188, 550–551
minima, 164–188, 344, 345, 346, 347
mustelina, 164–188
occidentalis, 302

ustulata, 164–188
Catoptrophorus semipalmatus, 440, 442, 443
Catostomus tahoensis, 556
Centrocercus urophasianus, 376
Cepphus columba, 441
grylle, 279–280
Cerorhinca monocerata, 441
Certhia brachydactyla, 59
familiaris, 59, 218–242, 273, 344
Certhidae, 67–76
chachalaca, see Ortalis vetula
Chaetura pelagica, 77–84
Chaffinch, see Fringilla coelebs
Chancellor, John, Audubon. A biography, reviewed, 293–294
Charadrius alexandrinus nivosus, 439
Chat, Yellow-breasted, see Icteria virens
Chen caerulescens, 548
Chickadee, Black-capped, see Parus atricapillus
Boreal, see Parus hudsonicus
Carolina, see Parus carolinensis
Chiffchaff, see Phylloscopus collybita
Chloris chloris, 265
Chlorospingus ophthalmicus, 278
Chordeiles minor, 547–548
Chub, tui, see Gila bicolor
Chubbia sp., 471
Chuck-will's-widow, see Caprimulgis carolinensis
Ciconia ciconia, 147
Cissilopha beecheii, 539
sanblasiana, 539
yucatanica, 539
Cisticola spp., 301
Clangula hyemalis, 110–111
Clark, E. Scott, Juvenile Peregrine Falcon swoops on Roseate Spoonbills, 548
Clark, George A., Toe fusion in oscines, 67–76
includes table of 55 oscine families, 69–72
Clark, Karen L. and Raleigh J. Robertson, Cowbird parasitism and evolution of anti-parasite strategies in the Yellow Warbler, 249–258
Clethrionomys glareolus, 291
Cnemidophorus sp., 94
cod, see Gadus macrocephalus
Colaptes auratus, 88, 218–242
Colbert, Edwin H., Evolution of the vertebrates, third edition, reviewed, 417
Coleoptera, 529, 554
Collins, Scott L., A comparison of nest-site and perch-site vegetation structure for seven species of warblers, 542–547
Columba livia, 109, 281, 357–362, 505
Conservation Committee (1980), Report on 1980, the year of the coast: birds, 438–456
Contopus virens, 218–242
Cooke, Fred, see Abraham, Kenneth F., Pierre Mineau and ———
Cooper, James A. and Alan D. Afton, A multiple sensor system for monitoring avian nesting behavior, 325–333
Cooper, Robert J., Relative abundance of Georgia caprimulgids based on call-counts, 363–371
Coot, American, see Fulica americana americana
Cormorant, Double-breasted, see Phalacrocorax auritus
Great, see Phalacrocorax carbo
cormorants, see Phalacrocorax spp.
Corvus brachyrhynchos, 344, 394, 395
corax, 344, 528
macrorhynchos, 280
splendens, 280
Corvus spp., 550
Coryagyps auratus, 97
Cossypha natalensis, 392
Cowbird, Bronzed, see Molothrus aeneus
Brown-headed, see Molothrus ater
Crake, Black-banded, see Laterallus [Anurolimnas] "hauxwelli" (=fasciatus)
Chestnut-headed, see Anurolimnas [Rallina] castaneiceps
Columbian, see Neocrex columbianus
Dot-winged, see Laterallus [Porzana] spilopterus
Gray-breasted, see Laterallus exilis
Paint-billed, see Neocrex erythrops
Red-and-White, see Laterallus leucopyrrhus
Ruddy, see Laterallus ruber
Rufous-faced, see Laterallus xenopterus
Rufous-sided, see Laterallus melanophaius
Russet-crowned, see Laterallus [Anurolimnas] viridis

Rusty-flanked, see Laterallus levraudi
Uniform, see Amaurolimnas concolor
Cramp, Stanley (ed.), Handbook of the birds of Europe, the Middle East, and North Africa. The birds of the Western Palearctic. Vol. 1, Ostrich to ducks. Vol. 2, Hawks to bustards, reviewed, 430–432
Crane, Florida Sandhill, see Grus canadensis pratensis
Greater Sandhill, see Grus canadensis tabida
Hooded, see Grus monacha
Japanese, see Grus japonensis
Sandhill, see Grus canadensis
White-naped, see Grus vipio
Whooping, see Grus americana
craneflies, see Tipulidae
crappie, white, see Pomoxis annularis
Crawford, Robert L., Weather, migration and autumn bird kills at a north Florida TV tower, 189–195
Creeper, Brown, see Certhia familiaris
Crocethia alba, 446
Crocoll, Scott and James W. Parker, Protocalliphora infestation in Broad-winged Hawk, 110
Crompton, Robert C., see Bellrose, Frank C. and ———
Crossbill, Red, see Loxia curvirostra
White-winged, see Loxia leucoptera
Crow, Common, see Corvus brachyrhynchos
House, see Corvus splendens
Large-billed, see Corvus macrorhynchos
Cruickshank, Allan D., The birds of Brevard County (edited by Helen G. Cruickshank), reviewed, 300
Curlew, Bristle-thighed, see Numenius tahitiensis
Curtis, Jane and Will, Welcome the birds to your home, reviewed, 300
Cyanocitta cristata, 164–188, 218–242, 334, 538–540, 551
stelleri, 539, 551
Cyanocorax yncas, 538–540
Cygnus cygnus buccinator, 330
olor, 443
Cyprinus carpio, 556
Cypseloides niger, 83
D'Agostino, Gloria M., Lorraine E. Giovinazzo and Stephen W. Eaton, The sentinel crow as an extension of parental care, 394–395
Dailey, Nancy S., see Avery, Michael L., Paul F. Springer and ———
Daption capense, 5–20
DeBenedictis, Paul A., review by, 428–430
deer, white-tailed, see Odocoileus virginianus
mule, see Odocoileus hemionus
DeGraff, Richard M. (Tech. Coord.), Proceedings of the workshop management of southern forests for nongame birds, reviewed, 292–293
Dellinger, Rebecca M., see Pulich, Warren M. and ———
Dendragapus obscurus, 291, 376
Dendrocopos pubescens, 218–242
villosus, 218–242
Dendrocygna autumnalis, 551–554
Dendroica caerulescens, 218–242
canadensis, 164–188, 218–242, 478
castanea, 240
cerulea, 478
coronata, 88, 334–339, 551
discolor, 164–188, 218–242, 295
dominica, 218–242
fusca, 218–242, 478
kirtlandii, 251, 295
magnolia, 164–188, 240
nigrescens, 164–188
palmarum, 542–547
pensylvanica, 36, 218–242, 478, 542–547
petechia, 218–242, 249–258, 542–547
pinus, 218–242
striata, 344–347
virens, 164–188, 218–242, 334–339, 478–490
DeSante, David F. and David G. Ainley, The avifauna of the South Farallon Islands, California, reviewed, 428–430
Deshotels, Jack H., see Guillory, D. and ———
Dichromanassa rufescens, 145–163
Dickcissel, see Spiza americana
Didelphis virginianus, 560
Diomedea chrysostoma, 5–20
exulans, 5–20
immutabilis, 445
melanophris, 5–20
nigripes, 445

Diomedea spp., 439, 445, 446
Dipodomys sp., 94
distribution
  Cyanocitta cristata, 540
  Cyanocorax yncas, 540
  Fulica americana americana, 115–118
  Laterallus sp., 140–141
  of Zone-tailed Hawks in west Texas, 282–284
Dove, Mourning, see Zenaida macroura
  Rock, see Columba livia
Dryocopus pileatus, 218–242
Duck, Black, see Anas rubripes
  Black-bellied Whistling, see Dendrocygna autumnalis
  Mallard, see Anas platyrhynchos
  Oldsquaw, see Clangula hyemalis
  Redhead, see Aythya americana
  Ring-necked, see Aythya collaris
  Ruddy, see Oxyura jamaicensis
  steamer, see Tachyeres sp.
  Wood, see Aix sponsa
Dumetella carolinensis, 104, 164–188, 218–242
Eagle, Bald, see Haliaeetus leucocephalus
  Black, see Aquila verreauxi
  Crested, see Morphnus guianensis
  Golden, see Aquila chrysaetos
  Harpy, see Harpia harpyja
  Lesser-spotted, see Aquila pomarina
Eaton, Stephen W., see D'Agostino, Gloria M., Lorraine E. Giovinazzo and ———
Eciton sp., 392
Editor's acknowledgments, 135
eggs
  Amaurolimnas concolor, 108
  Brachyramphus marmoratus, 400–403
  moving by female Gadwalls, 276–277
Egret, Cattle, see Bubulcus ibis
  Reddish, see Dichromanassa rufescens
  Snowy, see Egretta thula
Egretta sacra, 147, 153
  thula, 392
Eider, Common, see Somateria mollissima
Elanoides forficatus, 391
Eleutherodactylus sp., 107
Ellis, David H. and Wayne H. Whaley, Three Crested Eagle reports for Guatemala, 284–285
Emberizidae, 67–76
Empidonax difficilis, 412–414
  flavescens, 412–414
  flaviventris, 344
  virescens, 218–242, 478–490
Empidonax spp., 301
Enderson, James H., review by, 571–572
Endomychura hypoleuca, 439
Eremophila alpestris, 519–530
ermine, see Mustela erminea
errata
  for Williams, J. B., Vol. 92, No. 4, 163
  for Clark, K. L. and R. J. Robertson, Vol. 93, No. 2, 574
Estrilda astrild, 281–282
  erythronotos, 281
Eudocimus albus, 148–163
Euphagus carolinus, 344
Euthlypis lachrymosa, 392
Evans, H. E., see Baumel, J. J., et al.
Falco eleonorae, 287
  peregrinus, 548, 571–572
  peregrinus pealei, 572
Falcon, Eleonora's, see Falco eleonorae
  Peale's, see Falco peregrinus pealei
  Peregrine, see Falco peregrinus
falcons, see Micrastur sp.
Fawver, Ben J., see Kendeigh, S. Charles and ———
Feduccia, Alan, see Olson, Storrs L. and ———
———, The age of birds, reviewed, 407–412
Felis domestica, 528
Ferguson, Robert S., Territorial attachment and mate fidelity by Horned Grebes, 560–561
Fiala, Kent L., Survival of demaxillate Red-winged Blackbird, 563–565
Ficken, Millicent S., Food finding in Black-capped Chickadees: altruistic communication?, 393–394
Fieldfare, see Turdus pilaris
Finch, Purple, see Carpodacus purpureus
Fire-eyes, White-winged, see Pyriglena leucoptera
Fitch, Mary A., see Shugart, Gary W., ——— and Vern M. Shugart
Fitzpatrick, John W., review by, 412–414
flamingo, see Phoenicopteridae
Flicker, Common, see Colaptes auratus
Florida caerulea, 145–163

Flycatcher, Acadian, see Empidonax virescens
Great-crested, see Myiarchus crinitus
Kiskadee, see Pitangus sulphuratus
Western, see Empidonax difficilis
Yellow-bellied, see Empidonax flaviventris
Yellowish, see Empidonax flavescens
foraging, see behavior, food-related
Formicivora iheringi, 106
fox, red, see Vulpes vulpes
Franks, Edwin C., see Zammuto, Richard M. and ———
Fratercula arctica, 110, 341, 444, 572
Fregata magnificens, 439
minor palmerstonia, 445
French, Thomas W., Fish attack on Black Guillemot and Common Eider in Maine, 279–280
Fretwell, Stephen D. and Frank S. Shipley, Statistical significance and density-dependent nest predation, 541–542
Fries, Waldemar, The double elephant folio. The story of Audubon's birds of America, reviewed, 293–294
frigatebird, see Fregata minor palmerstoni
Magnificent, see Fregata magnificens
Fringilla coelebs, 123
frog, see Eleutherodactylus sp.
Fulica americana americana, 115–118, 274–275
Fulmar, Southern, see Fulmarus glacialoides
Southern Giant, see Macronectes giganteus
fulmars, see Fulmarus spp.
Fulmarus glacialoides, 12
Fulmarus spp., 443, 446
Gadus macrocephalus, 279
Gadwall, see Anas strepera
Galeocerdo cuvieri, 279
Gallinule, Purple, see Porphyrula martinica
gannets, see Morus spp.
Garbutt, Alan, The shoulder-spot display in Ruffed Grouse, 98–99
Gavia spp., 446
Geothlypis trichas, 218–242, 542–547
Gila bicolor, 555–556
Giovinazzo, Lorraine E., see D'Agostino, Gloria M., ——— and Stephen W. Eaton
Gnatcatcher, Blue-gray, see Polioptila caerulea
Godwit, Marbled, see Limosa fedoa
Goldfinch, American, see Spinus tristis
Gooders, John, see Alden, Peter and ———
Goose, Canada, see Branta canadensis interior and B. c. maxima
Greylag, see Anser anser
Lesser Snow, see Anser caerulescens caerulescens
Snow, see Chen caerulescens
Gorenzel, Warner P., Ronald A. Ryder and Clait E. Braun, American Coot distribution and migration in Colorado, 115–118
Graber, Richard R., review by, 572–573
Grackle, Common, see Quiscalus quiscula
Great-tailed, see Quiscalus mexicanus
Grant, C. H. B., see Mackworth-Praed, C. W. and ———
grasshoppers, see Orthoptera
Grassquit, Blue-black, see Volatinia jacarina
Grebe, Horned, see Podiceps auritus
Western, see Aechmophorus occidentalis
grebes, see Podicipedidae
Greenfinch, European, see Chloris chloris
Griffin, Curtice R., Interactive behavior among Bald Eagles wintering in north-central Missouri, 259–264
Griscom, Ludlow and Alexander Sprunt, Jr. (eds.), The warblers of America. Updated by Edgar M. Reilly, Jr., reviewed, 294–295
Grosbeak, Pine, see Pinicola enucleator
Rose-breasted, see Pheucticus ludovicianus
Ground-Thrush, Spotted, see Turdus fisheri
Grouse, Black, see Lyrurus tetrix
Blue, see Dendragapus obscurus
Hazel, see Tetrastes bonasia
Red, see Lagopus lagopus
Ruffed, see Bonasa umbellus
Sage, see Centrocercus urophasianus
Severtzor's Hazel, see Tetrastes sewerzowi
Sharp-tailed, see Pedioecetes phasianellus
Spruce, see Canachites canadensis
Grus americana, 100

canadensis, 99–103
canadensis pratensis, 100
canadensis tabida, 100
japonensis, 99, 101
monacha, 100
vipio, 100
Guillemot, Black, see Cepphus grylle
Pigeon, see Cepphus columba
Guillory, D. and Jack H. Deshotels, House Sparrows flushing prey from trees and shrubs, 554
Gull, Bonaparte's, see Larus philadelphia
Glaucous-winged, see Larus glaucescens
Herring, see Larus argentatus
Laughing, see Larus atricilla
Mew, see Larus canus
Ring-billed, see Larus delawarensis
Gullion, Gordon W., Non-drumming males in a Ruffed Grouse population, 372–382
gulls, see Larus spp.
Gymnopithys bicolor, 572
habitat structure
of warblers, 542–547
Haematopus spp., 441
Haematosiphon indorus, 110
Haliaeetus leucocephalus, 102, 109, 149, 259–264
Halichoerus grypus, 279
Hall, George A., review by, 425–427
Halobaena caerulea, 5–20
Hamerstrom, Frances, Strictly for the chickens, reviewed, 424
Harpia harpyja, 284–285
Harris, James T., The Peregrine Falcon in Greenland: observing an endangered species, reviewed, 129–131
Hawk, Broad-winged, see Buteo platypterus
Cooper's, see Accipiter cooperii
Ferruginous, see Buteo regalis
Red-shouldered, see Buteo lineatus
Red-tailed, see Buteo jamaicensis
Rough-legged, see Buteo lagopus
Sharp-shinned, see Accipiter striatus
Zone-tailed, see Buteo albonotatus
Hayward, Jim, Lovebirds and their color mutations, reviewed, 297–298
Heintzelman, Donald S., A manual for bird watching in the Americas, reviewed, 299
———, Hawks and owls of North America, reviewed, 129
———, North American ducks, geese and swans, reviewed, 133–134
Helmitheros vermivorus, 164–188, 218–242
Hensler, G. L. and J. D. Nichols, The Mayfield method of estimating nesting success: a model, estimators and simulation results, 42–53
Heppner, Frank H., see Preble, David E. and ———
Heron, Black-crowned Night, see Nycticorax nycticorax
Goliath, see Ardea goliatha
Green, see Butorides virescens
Grey, see Ardea cinerea
Little Blue, see Florida caerulea
Louisiana, see Hydranassa tricolor
Pond, see Ardeola greyii
Reef, see Egretta sacra
Squacco, see Ardeola ralloides
Hickman, Scott, Evidence for aerodynamic advantages of tail keeling in the Common Grackle, 500–505
Hirundinidae, 67–76
Hirundo rustica, 506, 507, 514
hog, feral, see Sus scrofa
Holmgren, Mark, review by, 299–300
Hoplopterus sp., 570
Houston, C. Stuart, Nature Saskatoon: an account of the Saskatoon Natural History Society, 1955–1980, reviewed, 574
Howard, Richard and Alick Moore, A complete checklist of the birds of the world, reviewed, 437
Howell, Thomas R., Breeding biology of the Egyptian Plover, Pluvianus aegyptius, reviewed, 570–571
Hummingbird, Black-chinned, see Archilochus alexandri
Hermit, 572
Long-tailed Hermit, see Phaethornis superciliosus
Ruby-throated, see Archilochus colubris
hybridization
in jays, 538–540
in teals, 403–405
Hydranassa tricolor, 145–163
Hydrobatidae, 439, 445, 446

Hydrophilus triangularis, 553
Hydrurga leptonyx, 9
Hylocichla guttata, 164–188, 550–551
  mustelina, 218–242
Ibis, Sacred, see Threskiornis aethiopica
  Straw-necked, see Threskiornis spinicollis
  White, see Eudocimus albus
  White-faced, see Plegadis chihi
Ictalurus nebulosus, 556
Icteria virens, 164–188, 218–242
Icteridae, 67–76, 94
Icterus cucullatus, 533, 535
  galbula, 533–535
  gularis, 531–537
Ixobrychus exilis, 145, 395–397
jackrabbit, black-tailed, see Lepus californicus
Jackson, Jerome A. (ed.), The "mid-south bird notes" of Ben B. Coffey, Jr., reviewed, 573
jaeger, see Stercorarius spp.
James, Ross D., review by, 424
Jarvis, Robert L., see Krapu, Gary L. and ———
Jay, Beechey's, see Cissilopha beecheii
  Blue, see Cyanocitta cristata
  Gray, see Perisoreus canadensis
  Green, see Cyanocorax yncas
  Magpie, see Calocitta formosa
  Mexican, see Aphelocoma ultramarina
  Purplish-backed, see Cissilopha beecheii
  San Blas, see Cissilopha sanblasiana
  Scrub, see Aphelocoma coerulescens
  Steller's, see Cyanocitta stelleri
  White-tipped Brown, see Psilorhinus morio
  Yucatan, see Cissilopha yucatanica
Johnson, Ned K., Character variation and evolution of sibling species in the Empidonax difficilis-flavescens complex (Aves: Tyrannidae), reviewed, 412–414
Johnson, Oscar W., review by, 570–571
Johnson, R., review by, 126–128
Johnson, Stephen R., review by, 298
Junco, Dark-eyed, see Junco hyemalis
  Gray-headed, see Junco caniceps
Junco caniceps, 551
  hyemalis, 164–188, 218–242, 344
Junco spp., 301
juncos, see Junco spp.
Karmali, John, Birds of Africa, reviewed, 436–437
Karr, James R., review by, 289
Kear, Janet and Andrew J. Berger, The Hawaiian Goose: an experiment in conservation, reviewed, 417–419
Keast, A. and E. S. Morton (eds.), Migrant birds in the neotropics: ecology, behavior, distribution, and conservation, reviewed, 432–435
Keith, Stuart, reviews by, 128–129, 430–432
Kendeigh, S. Charles and Ben J. Fawver, Breeding bird populations in the Great Smoky Mountains, Tennessee and North Carolina, 218–242
Kennedy, Joseph L., see Knopf, Fritz L. and ———
Kiff, Lloyd F., Eggs of the Marbled Murrelet, 400–403
Kilham, Lawrence, Agonistic behavior of the White-breasted Nuthatch, 271–274
———, Courtship feeding and copulation of Royal Terns, 390–391
King, A. S. and J. McLelland (eds.), Form and function in birds. Vol. 1, reviewed, 416–417
———, see Baumel, J. J., et al.
Kingbird, Eastern, see Tyrannus tyrannus
  Tropical, see Tyrannus melancholicus
kingbirds, see Tyrannus spp.
Kinglet, Golden-crowned, see Regulus satrapa
Kite, Swallow-tailed, see Elanoides forficatus
Kittiwake, Red-legged, see Rissa brevirostris
kittiwakes, see Rissa spp.
kleptoparasitism
  by waterfowl on American Coots, 274–275
Knodel-Montz, Janet Jean, Use of artificial perches on burned and unburned tallgrass prairie, 547–548
Knopf, Fritz L. and Joseph L. Kennedy, Differential predation by two species of piscivorous birds, 554–556
Knot, Red, see Calidris canutus
Krapu, Gary L. and Robert L. Jarvis, Effects of Redhead nest parasitism on Mallards, 562–563

Kushlan, James A., Resource use strategies of wading birds, 145–163
Lagopus lagopus, 376, 462, 571
leucurus, 376
Laing, Hamilton M., Allan Brooks: artist naturalist, reviewed, 422–423
Laniidae, 67–76
Lansdowne, J. F., Birds of the west coast. Vol. II, reviewed, 427–428
Lark, Horned, see Eremophila alpestris
Larus argentatus, 110–111, 505, 557, 567, 568
atricilla, 390
canus, 111, 112
delawarensis, 110
glaucescens, 111, 112
philadelphia, 111, 112
Larus spp., 123, 441, 446, 565
Laterallus albigularis, 141–144
exilis, 141–144 (Frontispiece)
fasciatus, 141–144
jamaicensis, 137–144, 443
leucopyrrhus, 137–144 (Frontispiece)
levraudi, 141–144
melanophaius, 137–144 (Frontispiece)
ruber, 141–144
spilonotus, 141–144
spilopterus, 141–144
viridis, 141–144
xenopterus, 137–144 (Frontispiece)
Laterallus spp., 108
Leafscraper, Scaly-throated, see Sclerurus guatemalensis
Lein, M. Ross, Display behavior of Ovenbirds (Seiurus aurocapillus) II. Song variation and singing behavior, 21–41
Lepidoptera, 554
Leptoptilos crumeniferus, 157
Lepus californicus, 93
Lill, Alan, review by, 414–416
Limnocryptes minimus, 472
Limnothlypis swainsonii, 164–188, 295
Limosa fedoa, 440
lizards, see Anolis sp.
see Cnemidophorus sp.
see Phrynosoma sp.
Lokemoen, John T. and David E. Sharp, First documented Cinnamon Teal nesting in North Dakota produced hybrids, 403–405
loons, see Gavia spp.
Lovell, T. W. I. (ed.), Woodland grouse symposium, reviewed, 290–292
Low, Rosemary, Parrots, their care and breeding, reviewed, 296–297
Loxia curvirostra, 344
leucoptera, 344
Lucas, A. M., see Baumel, J. J., et al.
Lumsden, Harry G., review by, 290–292
Lycosidae, 107, 529, 540
Lyrurus tetrix, 290, 376
Macaca sp., 391
Mackworth-Praed, C. W. and C. H. B. Grant, African handbook of birds: series one. Birds of eastern and north eastern Africa. Second ed., reviewed, 437
Macronectes giganteus, 5–20
Magpie, Black-billed, see Pica pica
manatee, see Trichechus manatus
Mares, Michael A., review by, 420–422
Martin, Robert F., Reproductive correlates of environmental variation and niche expansion in the Cave Swallow in Texas, 506–518
mate fidelity
Podiceps auritus, 560–561
Matteson, Sumner W. and John O. Riley, Distribution and reproductive success of Zone-tailed Hawks in west Texas, 282–284
Maurer, Brian A. and Robert C. Whitmore, Foraging of five bird species in two forests with different vegetation structure, 478–490
McGillivray, W. Bruce, Climatic influences on productivity in the House Sparrow, 196–206
McKay, Wallace D., Notes on Purple Gallinules in Colombian ricefields, 267–271
McLandress, M. Robert, Scrub Jay captures Hermit Thrush in flight, 550–551
——— and Dennis G. Raveling, Hyperphagia and social behavior of Canada Geese prior to spring migration, 310–324
McLelland, J., see King, A. S. and ———
McNair, Douglas B., Common Eider plays "possum," 559–560

Meadowlark, Eastern, see Sturnella magna
Meehan, Thomas E., see Siegel-Causey, Douglas and ———
meetings and conferences
annual meeting, The Wilson Ornithological Society, 1981, 135
proceedings WOS annual meeting 1981, 575–588
annual meeting, 1982, 477
fifth annual meeting of the Colonial Waterbird Group, 136
seventh international conference on bird census work and fifth meeting of the European Atlas Committee, 76
southeastern coastal and estuarine birds conference-workshop, 136
third international congress of ecology, 206
Melacoptila panamensis, 572
Melanerpes chrysauchen, 572
Melanotis caerulescens, 392
Melospiza georgiana, 164–188, 265, 344, 347
lincolnii, 164–188, 265–267
melodia, 255, 265
Menon, G. K., Cattle Egrets feeding in association with human workers, 549–550
Mengel, Robert M., reviews by, 293–294, 422–423
Merganser, Auckland, see Mergus australis
Red-breasted, see Mergus serrator
mergansers, see Mergus sp.
Mergus australis, 289
serrator, 445
Mergus sp., 392
Merritt, P. G., Narrowly disjunct allopatry between Black-capped and Carolina chickadees, 54–66
Micrastur sp., 279
Microtus pennsylvanicus, 528
migration
and autumn tower kills, in relation to weather, 189–195
Branta canadensis, 310–324
Fulica americana americana, 115–118
of passerines in relation to age, 164–188
Mimidae, 67–76
Mimus polyglottos, 266
Mineau, Pierre, see Abraham, Kenneth F., ——— and Fred Cooke
minimizing observational disturbance of colonial birds, 565–569
mink, see Mustela vison
Mniotilta varia, 164–188, 218–242, 278
Mockingbird, Blue, see Melanotis caerulescens
Northern, see Mimus polyglottos
Molothrus aeneus, 535, 536
ater, 249–258, 389, 547–548
Molothrus sp., 295
monkey, see Macaca sp.
monkfish, see Squatina squatina
Moore, Alick, see Howard, Richard and ———
moose, see Alces alces
Morphnus guianensis, 284–285
Morse, Douglas H., Foraging speeds of warblers in large populations and in isolation, 334–339
———, review by, 419–420
Morton, E. S., see Keast, A. and ———
Morton, Martin L., see Baptista, Luis F., ——— and Marie E. Pereyra
Morus spp., 443
Motacilla spp., 301
moth, see Lepidoptera
Moulton, Daniel W., Reproductive rate and renesting of Red-winged Blackbirds in Minnesota, 119–121
Mueller, Helmut C., Daniel D. Berger and George Allez, Age and sex differences in wing loading and other aerodynamic characteristics of Sharp-shinned Hawks, 491–499
——— and Nancy S. Mueller, Observations of a brood of Sharp-shinned Hawks in Ontario, with comments on the functions of sexual dimorphism, 85–92
Mueller, Nancy S., see Mueller, Helmut C. and ———
Murphy, Joseph R., see Tomback, Diana F. and ———
Murray, Robert K., Symbiotic interaction between Starlings and deer, 549
Murrelet, Ancient, see Synthliboramphus antiquus
Kittlitz's, see Brachyramphus brevirostris
Marbled, see Brachyramphus marmoratus
Xantus, see Endomychura hypoleuca
Mustela erminea, 528
vison, 528

Mycteria americana, 146–163
Myiarchus crinitus, 218–242
Myioborus miniatus, 278
Myrmeciza longipes, 105
  loricata, 105
Neocrex columbianus, 141
  erythrops, 141
Nesbitt, Stephen A. and G. W. Archibald, The agonistic repertoire of Sandhill Cranes, 99–103
nest
  of Amaurolimnas concolor, 108
  of Eremophila alpestris, 523–524
  of Icterus gularis, 532–533
  site selection by penguins, 243–248
nesting
  association
    between Icterus gularis and large tyrannid flycatchers, 535–536
  density
    statistical significance of the effect on nest predation, 541–542
  success
    estimation of, 42–53
nestling
  feeding of
    Accipiter striatus, 85–94
  temperature regulation of
    Buteo regalis, 92–97
Newton, Ian, Population ecology of raptors, reviewed, 286–288
niche
  expansion
    Petrochelidon fulva, 506–518
  separation
    Turdus sp., 112–114
Nichols, J. D., see Hensler, Gary L. and ———
Nighthawk, Common, see Chordeiles minor
Nightingale-Thrush, Ruddy-capped, see Catharus frantzii
  Russet, see Catharus occidentalis
Nolan, Val, Jr., review by, 294–295
Numenius tahitiensis, 445
Nuthatch, Pygmy, see Sitta pygmaea
  Red-breasted, see Sitta canadensis
  White-breasted, see Sitta carolinensis
Nycticorax nycticorax, 150
Nye, Peter E., see Stone, Ward B. and ———
Oceanites oceanicus, 5–20
octopus, see Octopus sp.
Octopus sp., 279
Odocoileus hemionus, 549
  virginianus, 549
Olson, Storrs L. and Alan Feduccia, Presbyornis and the origin of the Anseriformes (Aves: Charadriomorphae), reviewed, 407–412
——— and ———, Relationships and evolution of flamingos (Aves: Phoenicopteridae), reviewed, 407–412
Oncorhynchus gorbusche, 111
O'Neill, John P., review by, 427–428
Oniki, Yoshika, see Willis, Edwin O. and ———
Oporornis agilis, 164–188
  formosus, 164–188, 218–242
  philadelphia, 164–188
opossum, see Didelphis virginianus
Orcinus orca, 10
Oren, David C. and Nigel J. H. Smith, Notes on the status of the Common African Waxbill in Amazonia, 281–282
Oriole, Hooded, see Icterus cucullatus
  Lichtenstein's, see Icterus gularis
  Northern, see Icterus galbula
Ortalis vetula, 536
Orthoptera, 534, 540
Oryzoborus angolensis, 282
Otus spp., 301
Ovenbird, see Seiurus auricapillus
Owl, Barred, see Strix varia
  Great-horned, see Bubo virginianus
  Long-eared, see Asio otus
  Short-eared, see Asio flammeus
owls, see Otus spp.
oxpeckers, see Buphagus spp.
Oxyura jamaicensis, 330, 331, 443
oystercatchers, see Haematopus spp.
Pachyptila desolata, 5–20
Pagodroma nivea, 5–20
parasites
  Haematosiphon indorus, 110
  Protocalliphora in Buteo platypterus, etc., 110
  Trichomoniasis in Haliaeetus leucocephalus, etc., 109
parasitism
  of Aythya americana on Anas platyrhyncos, 562–563

of Molothrus aeneus on Icterus gularis, 535
of Molothrus ater on Dendroica petechia, 249–258
Paridae, 67–76
Parker, James W., see Crocoll, Scott and ———
Partridge, Grey, see Perdix perdix
Parula, Northern, see Parula americana
Tropical, see Parula americana pulchra
Parula americana, 218–242, 344, 542–547
americana insularis, 306
americana pulchra, 306
pitiayumi, 306
Parula spp., 306
Parulidae, 67–76
Parus atricapillus, 54–66, 218–242, 273, 344, 346, 347, 393, 394
bicolor, 63, 218–242
carolinensis, 54–66, 218–242
hudsonicus, 344, 345, 346, 347
Passer domesticus, 196–206, 281, 551, 554
Passerculus sandwichensis, 344
Passerella iliaca, 164–188, 344, 346
Passerina amoena, 59, 265
cyanea, 59, 218–242, 265
Pedioecetes phasianellus, 330, 376
Pelecanus erythrorhynchos, 554–556
occidentalis, 439, 445
occidentalis californicus, 397
occidentalis carolinensis, 397
occidentalis occidentalis, 397–400
Pelican, Brown, see Pelecanus occidentalis
White, see Pelecanus erythrorhynchos
Penguin, Adélie, see Pygoscelis adeliae
Chinstrap, see Pygoscelis antarctica
Emperor, see Aptenodytes forsteri
Gentoo, see Pygoscelis papua
perch, Sacramento, see Archoplites interruptus
perches
use of artificial, 547–548
Percnostola rufifrons, 106
Perdix perdix, 292
Pereyra, Marie E., see Baptista, Luis F., Martin L. Morton and ———
Perisoreus canadensis, 88
Peterson, Roger Tory, Introduction and commentaries on: Audubon, birds of America, reviewed, 293–294
———, A field guide to the birds, fourth edition, reviewed, 425–427
Petrel, Antarctic, see Thalassoica antarctica
Blue, see Halobaena caerulea
Dark-rumped, see Pterodroma phaeopygia sandwichensis
Mottled, see Pterodroma inexpecta
Snow, see Pagodroma nivea
Petrochelidon fulva, 506–518
pyrrhonota, 514
Phaethon aetherus, 439
Phaethornis superciliosus, 414–416
Phalacrocorax auritus, 554–556
carbo, 357
Phalacrocorax spp., 441, 443, 446
Phalaenoptilus nuttallii, 363
Phalarope, Red, see Phalaropus fulicarius
phalaropes, see Phalaropodidae
Phalaropodidae, 446
Phalaropus fulicarius, 557
Pheucticus ludovicianus, 164–188, 218–242
Phillips, Allan R., Subspecies vs forgotten species: the case of Grayson's Robin (Turdus graysoni), 301–309 (Frontispiece)
Philohela spp., 471
Phoebe, Eastern, see Sayornis phoebe
Phoebetria palpebrata, 5–20
Phoenicopteridae, 407–412
Phrynosoma sp., 94
Phylloscopus collybita, 59
trochilus, 59
Phylloscopus spp., 301
Pica pica, 196, 550
Picoides pubescens, 63
villosus, 274
Pigeon, Cape, see Daption capense
Pinicola enucleator, 344
Pintail, see Anas acuta
Pipilo albicollis, 59
erythrophthalmus, 218–242
fuscus, 59
Pipilo spp., 301
Piranga olivacea, 164–188, 218–242, 478–490
Pitangus sulphuratus, 535–536
Pitelka, Frank A. (ed.), Shorebirds in marine environments, reviewed, 131–132
Pleasants, Barbara Yohai, Aspects of the breeding biology of a subtropical oriole, Icterus gularis, 531–537

Plectrophenax nivalis, 522
Plegadis chihi, 147
Plover, Egyptian, see Pluvialis aegyptius
Golden, see Pluvialis dominica fulva
Greater Golden, see Pluvialis apricaria
Snowy, see Charadrius alexandrinus nivosus
plovers, see Hoplopterus sp.
Pluvialis aegyptius, 570–571
apricaria, 560
dominica fulva, 445
Poché, Richard M., Crows steal golf balls in Bangladesh, 280
Podiceps auritus, 560–561
Podicipedidae, 446, 560
Polioptila caerulea, 218–242
Pomacea sp., 552, 553
Pomatomus saltatrix, 280
Pomoxis annularis, 556
Poor-will, see Phalaenoptilus nuttallii
population
density
caprimulgids, 363–371
passerine, 340–349
Porphyrula martinica, 267
Porzana spilopterus, 141
Porzana spp., 108
Powell, George V. N., review by, 425
Prairie Chicken, Attwater's, see Tympanuchus cupido attwateri
Greater, see Tympanuchus cupido
Preble, David E. and Frank H. Heppner, Breeding success in an isolated population of Rock Doves, 357–362
predation
by Aphelocoma coerulescens on Hylocichla guttata, 550–551
by Falco peregrinus on Ajaia ajaja, 548
on eggs and nestlings of Eremophila alpestris, 528
Presbyornis, 407–412
President's message, 264
Preston, Charles R., Environmental influence on soaring in wintering Red-tailed Hawks, 350–356
Prion, Antarctic, see Pachyptila desolata
productivity
of House Sparrows in relation to climate, 196–206
Protocalliphora avium, 110
Protonotaria citrea, 164–188
Psilorhinus morio, 539
Ptarmigan, White-tailed, see Lagopus leucurus
Willow, see Lagopus lagopus
Pterodroma inexpecta, 14
phaeopygia sandwichensis, 445
Ptychoramphus aleutica, 439
Puffin, Common, see Fratercula arctica
Puffinus griseus, 14, 439, 446
puffinus, 110
puffinus newelli, 445
tenuirostris, 446
Pulich, Warren M. and Rebecca M. Dellinger, An example of a hybrid Green Jay × Blue Jay, 538–540
Pygoscelis adeliae, 2–20, 243–248
antarctica, 243–248
papua, 243–248
Pyriglena leucoptera, 105, 106
Quiscalus mexicanus, 536
quiscula, 500–505
Raikow, Robert J., reviews by, 125–126, 299, 300, 407–412, 416, 417, 437, 573, 574
Rail, Black, see Laterallus jamaicensis
California Clapper, see Rallus longirostris obsoletus
Clapper, see Rallus longirostris
Galapagos, see Laterallus spilonotus
Gray-necked Wood, see Aramides cajanea
Rakestraw, James L. and James L. Baker, Dusky Seaside Sparrow feeds Red-winged Blackbird fledglings, 540
Rallina castaneiceps, 141
Rallus longirostris, 443
longirostris obsoletus, 440
Rallus spp., 108
Ralph, C. John, Age ratios and their possible use in determining autumn routes of passerine migrants, 164–188
rat, kangaroo, see Dipodomys sp.
Ratcliffe, Derek, The Peregrine Falcon, reviewed, 571–572
Raveling, Dennis G., see McLandress, M. Robert and ———
Raven, Common, see Corvus corax
Razorbill, see Alca torda
Redstart, American, see Setophaga ruticilla
Slate-throated, see Myioborus miniatus
Redwing, European, see Turdus iliacus

Regulus satrapa, 218–242, 344
renesting
of Agelaius phoeniceus, 119–121
reproductive rate
of Agelaius phoeniceus, 119–121
request for assistance
for study skins, skeletons and alcoholics, 569
resource use
by wading birds, 145–163
Rhodinocichla rosea, 392
Rhopornis ardesiaca, 103–107
Rice, Jake C., Behavioral implications of aberrant song of a Red-eyed Vireo, 383–390
———, see Vassallo, Monique I. and ———
Richards, Alan J., British birds—a field guide, reviewed, 128–129
Riley, John O., see Matteson, Sumner W. and ———
Ripley, S. Dillon, see Ali, Sálim and ———
Rissa brevirostris, 111–112
Rissa spp., 443
Robbins, Mark B., Two cases of commensal feeding between passerines, 391–392
Robertson, Raleigh J., see Clark, Karen L. and ———
Robin, American, see Turdus migratorius
Clay-colored, see Turdus grayi
Grayson's, see Turdus graysoni
Rufous-backed, see Turdus rufo-palliatus
White-throated, see Turdus phaeopygus
Robin-Chat, Red-capped, see Cossypha natalensis
roosting
of Chaetura pelagica, 77–84
Rostratula benghalensis, 469
Ryan, Mark R., Evasive behavior of American Coots to kleptoparasitism by waterfowl, 274–275
Ryder, Ronald A., see Gorenzel, Warner P., ——— and Clait E. Braun
Rynchops nigra, 444
Rynchops sp., 123, 441
salmon, humpbacked, see Oncorhynchus gorbusche
Sanderling, see Crocethia alba
Sandpiper, Spotted, see Actitis macularia
Upland, see Bartramia longicauda
Savage, Christopher (ed.), Pheasants in Asia, reviewed, 574
Sayornis phoebe, 164–188
Scatella stagnalis, 552, 553
Scaup, Lesser, see Aythya affinis
Schreiber, Ralph W., David W. Belitsky and Bruce A. Sorrie, Notes on Brown Pelicans in Puerto Rico, 397–400
Sclerurus guatemalensis, 392
Scolopax spp., 465, 471, 472
seal, grey, see Halichoerus grypus
leopard, see Hydrurga leptonyx
Seedeater, Chestnut-bellied, see Sporophila castaneiventris
Seedfinch, Lesser, see Oryzoborus angolensis
Seiurus auricapillus, 21–41, 218–242, 542–547
motacilla, 218–242
noveboracensis, 164–188, 344, 345, 346
Setophaga ruticilla, 188, 218–242, 295, 478–490
sexual dimorphism
Accipter striatus, 85–92
sharks, see Carcharinus leucas
see Carcharinus longimanus
see Carcharodon carcharias
see Galeocerdo cuvieri
Sharp, David E., see Lokemoen, John T. and ———
Shearwater, Manx, see Puffinus puffinus
Newell's, see Puffinus puffinus newelli
Slender-billed, see Puffinus tenuirostris
Sooty, see Puffinus griseus
Shipley, Frank S., see Fretwell, Stephen D. and ———
shorefly, see Scatella stagnalis
Shoveler, Northern, see Anas clypeata
shrew, see Sorex cinereus
Shugart, Gary W., Mary A. Fitch and Vern M. Shugart, Minimizing investigator disturbance in observational studies of colonial birds: access to blinds through tunnels, 565–569
Shugart, Vern M., see Shugart, Gary W., Mary A. Fitch and ———
Siala currucoides, 288
Siegel-Causey, Douglas and Thomas E. Meehan, Red-legged Kittiwakes for-

age in mixed species flocks in southeastern Alaska, 111–112
Siskin, Pine, see Carduelis pinus
Sitta canadensis, 218–242, 273, 344
carolinensis, 63, 218–242, see 271–274
europaea, 274
pygmaea, 551
Sittidae, 67–76
Skimmer, Black, see Rynchops nigra
skimmers, see Rynchops sp.
Skua, South Polar, see Catharacta maccormicki
skuas, see Catharacta spp.
Skutch, Alexander F., The imperative call: a naturalist's quest in temperate and tropical America, reviewed, 425
———, A naturalist on a tropical farm, reviewed, 572–573
Slud, Paul, The birds of Hacienda Palo Verde, Guanacaste, Costa Rica, reviewed, 435–436
Smith, Nigel J. H., see Oren, David C. and ———
snail, apple, see Pomacea sp.
Snell, Richard R., Herring Gull attacks and eats adult male Oldsquaw, 110–111
Snipe, African, see Capella gallinago nigripennis
Andean, see Capella jamesoni
Asiatic, see Capella stenura
Australian, see Capella hardwickii
Banded, see Capella imperialis
Bogotá, see Capella imperialis
Common, see Capella gallinago
Cordilleran, see Capella stricklandii
Double, see Capella media
English, 466, 467
Ethiopian, see Capella gallinago nigripennis
Fantail, see Capella gallinago
Forest, see Capella megala
Giant, see Capella undulata
Great, see Capella media
Hermit, see Capella solitaria
Himalayan, see Capella nemoricola
Imperial, see Capella imperialis
Jack, see Lymnocryptes minimus
Japanese, see Capella hardwickii
Lathmans, see Capella hardwickii
Madagascar, see Capella macrodactyla
Marsh, see Capella megala
Noble, see Capella nobilis
Painted, see Rostratula benghalensis
Paramo, see Capella nobilis
Pintail, see Capella stenura
Silent, see Lymnocryptes minimus
Single, see Capella gallinago
Solitary, see Capella solitaria
Swinhoe's, see Capella megala
Wilson's, see Capella gallinago
Wood, see Capella nemoricola
Softwing, White-whiskered, see Melacoptila panamensis
Somateria mollissima, 279, 559–560
Somateria sp., 290
song
Amaurolimnas concolor, 107
mimesis by Melospiza lincolnii, 265–267
Rhopornis ardesiaca, 105–106
Seiurus aurocapillus, 21–41
Songthrush, see Turdus philomelos
Sorex cinereus, 528
Sorrie, Bruce A., see Schreiber, Ralph W., David W. Belitsky and ———
Soulé, Michael E. and Bruce A. Wilcox (eds.), Conservation biology: an evolutionary-ecological perspective, reviewed, 420–422
Sparrow, Chipping, see Spizella passerina
Dusky Seaside, see Ammospiza maritima nigrescens
Field, see Spizella pusilla
Fox, see Passerella iliaca
Grasshopper, see Ammodramus savannarum
House, see Passer domesticus
Lincoln's, see Melospiza lincolnii
Rufous-collared, see Zonotrichia capensis
Savannah, see Passerculus sandwichensis
Seaside, see Ammospiza maritima
Sharp-tailed, see Ammospiza caudacuta
Song, see Melospiza melodia
Swamp, see Melospiza georgiana
White-crowned, see Zonotrichia leucophrys
White-throated, see Zonotrichia albicollis
Yellow-browed, see Ammodramus aurifrons

Sparrowhawk, see Accipiter nisus
species diversity
Newfoundland passerines, 340–349
Spermophilus richardsonii, 572
townsendii, 572
spider, see Lycosidae
Spinus tristis, 344, 346
Spiza americana, 547–548
Spizella passerina, 88
pusilla, 164–188, 218–242, 541
Spofford, Walter R., review by, 129
Spoonbill, Roseate, see Ajaia ajaja
Sporophila castaneiventris, 282
Springer, Paul F., see Avery, Michael L., ——— and Nancy S. Dailey
Sprunt, Alexander, Jr., see Griscom, Ludlow and ———
Squatina squatina, 279
squirrel, red, see Tamiasciurus hudsonicus
Richardson's ground, see Spermophilus richardsonii
Townsend's ground, see Spermophilus townsendii
Starling, see Sturnus vulgaris
status
of Estrilda astrid in Amazonia, 281–282
of Morphnus guianensis in Guatemala, 284–285
Stepney, Philip H. R. and Peter C. Boxall, First record of the Black-chinned Hummingbird in Alberta, 405–406
Stercorarius spp., 439, 443, 446
Sterna albifrons browni, 439
caspia, 567, 568
maxima, 390–391
paradisaea, 13
sandvicensis, 390
Sterna spp., 123, 392, 441, 445, 446
Stiles, F. Gary, Notes on the Uniform Crake in Costa Rica, 107–108
———, review by, 435–436
——— and Larry L. Wolf, Ecology and evolution of lek mating behavior in the Long-tailed Hermit Hummingbird, reviewed, 414–416
Stone, Ward B. and Peter E. Nye, Trichomoniasis in Bald Eagles, 109
Storer, Robert W., The Rufous-faced Crake (Laterallus xenopterus) and its Paraguayan congeners, 137–144 (Frontispiece)
Stork, Marabou, see Leptoptilos crumeniferus
White, see Ciconia ciconia
Wood, see Mycteria americana
Storm-petrel, Wilson's see Oceanites oceanicus
storm-petrels, see Hydrobatidae
Strix varia, 272
Sturnella magna, 547–548
Sturnus vulgaris, 344, 347, 549
sucker, Tahoe, see Catostomus tahoensis
Sula spp., 445
Sus scrofa, 549
Sutton, George Miksch, Commentary on, To a young bird artist: letters from Louis Agassiz Fuertes to Geroge Miksch Sutton, reviewed, 295–296
———, Iceland summer: adventures of a bird painter, reviewed, 299
———, On aerial and ground displays of the world's snipes, 457–477 (Frontispiece)
Swallow, Barn, see Hirundo rustica
Cave, see Petrochelidon fulva
Cliff, see Petrochelidon pyrrhonota
Swan, Mute, see Cygnus olor
Trumpeter, see Cygnus cygnus buccinator
Swift, Black, see Cypseloides niger
Chimney, see Chaetura pelagica
Common, see Apus apus
Sylvia atricapilla, 59
communis, 59
symbiosis
between Starlings and deer, 549
Synthliboramphus antiquus, 402
Szaro, Robert C. and Russell P. Balda, Bird community dynamics in a ponderosa pine forest, reviewed, 419–420
Tabor, James E., see Thompson, Bruce C. and ———
Tachyeres sp., 289
Tamiasciurus hudsonicus, 334
Tanager, Scarlet, see Piranga olivacea
Speckled, see Tangara guttata
Tangara guttata, 572
taxonomy
Laterallus spp., 137–144
Turdus graysoni, 301–309
Taylor, L. R., see Anderson, R. M., B. D. Turner and ———
Teal, Blue-winged, see Anas discors

Cinnamon, see Anas cyanoptera
Green-winged, see Anas crecca carolinensis
temperature regulation
in nesting Buteo regalis, 92–97
Tern, Arctic, see Sterna paradisaea
California Least, see Sterna albifrons browni
Caspian, see Sterna caspia
Royal, see Sterna maxima
Sandwich, see Sterna sandvicensis
terns, see Sterna spp.
Tetrao parvirostris, 290
urogallus, 290
Tetrastes bonasia, 290
sewerzowi, 290
Thalassoica antarctica, 5–20 (Frontispiece)
Theide, Walther, Water and shore birds, reviewed, 574
Thompson, Bruce C. and James E. Tabor, Mallard using moving vehicles for predator avoidance, 277–278
Thrasher, Brown, see Toxostoma rufum
Threlfall, William, see Cannings, Richard J. and ———
Threskiornis aethiopica, 148–163
spinicollis, 148
Thrush, Gray-cheeked, see Catharus minima
Hermit, see Catharus [Hylocichla] guttata
Swainson's, see Catharus ustulata
White-necked, see Turdus albicollis
Wood, see Catharus [Hylocichla] mustelina
Thrush-tanager, Rose-breasted, see Rhodinocichla rosea
Thryothorus ludovicianus, 218–242
Thurber, Walter A., Aerial "play" of Black Vultures, 97
Thyromanes bewickii, 59
Tipulidae, 529
Titmouse, Tufted, see Parus bicolor
toad, marine, see Bufo marinus
Tomback, Diana F. and Joseph R. Murphy, Food deprivation and temperature regulation in nestling Ferruginous Hawks, 92–97
tower kills, 189–195
Towhee, Brown, see Pipilo fuscus
Rufous-sided, see Pipilo erythrophthalmus
White-throated, see Pipilo albicollis
towhees, see Pipilo spp.
Toxostoma rufum, 164–188, 218–242
Traylor, Melvin A., review by, 436–437
tree creepers, see Certhia brachydactyla
see Certhia familiaris
Trichechus manatus, 400
Trichomonas gallinae, 109
Trivelpiece, Wayne, see Volkman, Nicholas J. and ———
Troglodytes aedon, 59
ochraceus, 278–279
troglodytes, 218–242, 344, 347
Troglodytidae, 67–76
Turdus albicollis, 112–114
assimilis, 302, 307
fisheri, 392
grayi, 302
graysoni, 301–309 (Frontispiece)
iliacus, 112–114
merula, 112–114
migratorius, 112–114, 164–188, 218–242, 344, 345, 346, 564
phaeopygus, 302, 303, 307
philomelos, 112–114
pilaris, 112–114
rufo-palliatus, 302–309
Turner, B. D., see Anderson, R. M., ——— and L. R. Taylor
Turnstone, Ruddy, see Arenaria interpres
Tye, Alan, Ground-feeding methods and niche separation in thrushes, 112–114
Tympanuchus cupido, 376, 424
cupido attwateri, 376
Tyrannus melancholicus, 535–536
tyrannus, 344, 547–548
Tyrannus spp., 302, 535
Ure, Stellanie, Hawk lady, reviewed, 423–424
van Riper, Charles, III, review by, 417–419
Vardaman, James M., Call collect, ask for birdman, review, 299–300
Vassallo, Monique I. and Jake C. Rice, Differential passerine density and diversity between Newfoundland and offshore Gull Island, 340–349
Vaughan, Richard, Arctic summer: birds in north Norway, reviewed, 298

Veery, see Catharus fuscescens
Verdin, see Auriparus flaviceps
Vermivora celata, 164–188, 295
  chrysoptera, 218–242, 295
  pinus, 164–188, 295
  ruficapilla, 164–188, 542–547
viper, tree, see Bothrops lateralis
Vireo, Red-eyed, see Vireo olivaceus
  Philadelphia, see Vireo philadelphicus
  Solitary, see Vireo solitarius
  White-eyed, see Vireo griseus
  Yellow-throated, see Vireo flavifrons
Vireo flavifrons, 218–242
  griseus, 218–242
  olivaceus, 164–188, 218–242, 383–390, 478–490
  philadelphicus, 188
  solitarius, 218–242
Vireonidae, 67–76
vocalization
  caprimulgids, 363–371
  Vireo olivaceus, 383–390
Volatinia jacarina, 282
vole, bank, see Clethrionomys glareolus
  meadow, see Microtus pennsylvanicus
Volkman, Nicholas J. and Wayne Trivelpiece, Nest-site selection among Adélie, Chinstrap and Gentoo penguins in mixed species rookeries, 243–248
Vulpes vulpes, 528
wagtails, see Motacilla spp.
Walter, Hartmut, review by, 129–131
Walters, Michael, The complete book of birds of the world, reviewed, 299
Wander, Wade, Red Phalarope eating carrion, 557
Warbler, Bay-breasted, see Dendroica castanea
  Black-and-white, see Mniotilta varia
  Blackburnian, see Dendroica fusca
  Blackpoll, see Dendroica striata
  Black-throated Blue, see Dendroica nigrescens
    see Dendroica caerulescens
  Black-throated Green, see Dendroica virens
  Canada, see Wilsonia [Dendroica] canadensis
  Cerulean, see Dendroica cerulea
  Chestnut-sided, see Dendroica pensylvanica
  Connecticut, see Oporornis agilis
  Fan-tailed, see Euthlypis lachrymosa
  Golden-crowned, see Basileuterus culicivorus
  Golden-winged, see Vermivora chrysoptera
  Hooded, see Wilsonia citrina
  Kentucky, see Oporornis formosus
  Kirtland's, see Dendroica kirtlandii
  Magnolia, see Dendroica magnolia
  Marsh, see Acrocephalus palustris
  Mourning, see Oporornis philadelphia
  Nashville, see Vermivora ruficapilla
  Orange-crowned, see Vermivora celata
  Palm, see Dendroica palmarum
  Parula, see Parula americana
  Pine, see Dendroica pinus
  Prairie, see Dendroica discolor
  Prothonotary, see Protonotaria citrea
  Reed, see Acrocephalus scirpaceus
  Swainson's, see Limnothlypis swainsonii
  Willow, see Phylloscopus trochilus
  Wilson's, see Wilsonia pusilla
  Worm-eating, see Helmitheros vermivorus
  Yellow, see Dendroica petechia
  Yellow-rumped, see Dendroica coronata
  Yellow-throated, see Dendroica dominica
warblers, see Cisticola spp.
  see Parula spp.
  see Phylloscopus spp.
wasp, 528
Waterthrush, Louisiana, see Seiurus motacilla
  Northern, see Seiurus noveboracensis
Waxbill, Black-cheeked, see Estrilda erythronotos
  Common African, see Estrilda astrild
Waxwing, Cedar, see Bombycilla cedrorum
Weller, Milton, The island waterfowl, reviewed, 289
whale, killer, see Orcinus orca
Whaley, Wayne H., see Ellis, David H. and
———
Whip-poor-will, see Caprimulgis vociferus
White, Clayton, review by, 286–288
Whitethroat, see Sylvia communis

Whitmore, Robert C., reviews by, 292–293, 432–435
———, see Maurer, Brian A. and ———
Whittemore, Margaret, Chimney Swifts and their relatives, reviewed, 573
Wigeon, American, see Anas americana
Wilcox, Bruce A., see Soulé, Michael E. and ———
Willet, see Catoptrophorus semipalmatus
Willis, Edwin O. and Yoshika Oniki, Notes on the Slender Antbird, 103–107
Wilsonia canadensis, 164–188, 218–242, 478
citrina, 164–188, 218–242
pusilla, 164–188, 278, 344
Wolf, Larry L., see Stiles, F. Gary and ———
woodcocks, see Philohela spp.
see Scolopax spp.
Woodpecker, Downy, see Picoides [Dendrocopos] pubescens
Golden-naped, see Melanerpes chrysauchen
Hairy, see Picoides [Dendrocopos] villosus
Pileated, see Dryocopus pileatus
Wood-rail, see Aramides sp.
Wren, Bewick's, see Thyromanes bewickii
Cactus, see Campylorhynchus brunneicapillus
Carolina, see Thryothorus ludovicianus
House, see Troglodytes aedon
Ochraceous, see Troglodytes ochraceus
Winter, see Troglodytes troglodytes
Yellowthroat, Common, see Geothlypis trichas
Zammuto, Richard M. and Edwin C. Franks, Environmental effects on roosting behavior by Chimney Swifts, 77–84
Zenaida macroura, 109
Zicus, Michael C., Canada Goose brood behavior and survival estimates at Crex Meadows, Wisconsin, 207–217
Zink, Robert M., Observations of seabirds during a cruise from Ross Island to Anvers Island, Antarctica, 1–20 (Frontispiece)
Zonotrichia albicollis, 344
capensis, 532
leucophrys, 169, 172
leucophrys oriantha, 265

This issue of *The Wilson Bulletin* was published on 22 February 1982.

7070 064

The Wilson Bulletin

Editor Jon C. Barlow

Department of Ornithology
Royal Ontario Museum
100 Queen's Park
Toronto, Ontario, Canada M5S 2C6

Assistant Editor Margaret L. May

Senior Editorial Assistants Gary Bortolotti
Nancy Flood

Editorial Assistants Keith L. Bildstein
C. Davison Ankney
Richard R. Snell
James D. Rising

Review Editor Robert Raikow
Department of Biological Sciences
University of Pittsburgh
Pittsburgh, PA 15260

Color Plate Editor William A. Lunk
865 North Wagner Road
Ann Arbor, MI 48103

Suggestions to Authors

See Wilson Bulletin, 91:366, 1979 for more detailed "Suggestions to Authors." Manuscripts intended for publication in *The Wilson Bulletin* should be submitted in triplicate, neatly typewritten, double-spaced, with at least 3 cm margins, and on one side only of good quality white paper. Do not submit xerographic copies that are made on slick, heavy paper. Tables should be typed on separate sheets, and should be narrow and deep rather than wide and shallow. Follow the AOU Check-list (Fifth Edition, 1957) and the 32nd Supplement (Auk, 90:411–419, 1973), insofar as scientific names of U.S. and Canadian birds are concerned. Summaries of major papers should be brief but quotable. Where fewer than 5 papers are cited, the citations may be included in the text. All citations in "General Notes" should be included in the text. Follow carefully the style used in this issue in listing the literature cited; otherwise, follow the "CBE Style Manual" (1972, AIBS). Photographs for illustrations should have good contrast and be on gloss paper. Submit prints unmounted and attach to each a brief but adequate legend. Do not write heavily on the backs of photographs. Diagrams and line drawings should be in black ink and their lettering large enough to permit reduction. Original figures or photographs submitted must be smaller than 22 × 28 cm. Alterations in copy after the type has been set must be charged to the author.

Notice of Change of Address

If your address changes, notify the Society immediately. Send your complete new address to Ornithological Societies of North America, % Sandra L. L. Gaunt, Box 21160, Columbus, Ohio 43221.

The permanent mailing address of the Wilson Ornithological Society is: c/o The Museum of Zoology, The University of Michigan, Ann Arbor, Michigan 48109. Persons having business with any of the officers may address them at their various addresses given on the back of the front cover, and all matters pertaining to the Bulletin should be sent directly to the Editor.

Membership Inquiries

Membership inquiries should be sent to Dr. Keith Bildstein, Department of Biology, Winthrop College, Rock Hill, South Carolina 29733.

CONTENTS

ON AERIAL AND GROUND DISPLAYS OF THE WORLD'S SNIPES ---------- *George Miksch Sutton* 457

FORAGING OF FIVE BIRD SPECIES IN TWO FORESTS WITH DIFFERENT VEGETATION STRUCTURE
Brian A. Maurer and Robert C. Whitmore 478

AGE AND SEX DIFFERENCES IN WING LOADING AND OTHER AERODYNAMIC CHARACTERISTICS OF SHARP-SHINNED HAWKS ------ *Helmut C. Mueller, Daniel D. Berger and George Allez* 491

EVIDENCE FOR AERODYNAMIC ADVANTAGES OF TAIL KEELING IN THE COMMON GRACKLE
Scott Hickman 500

REPRODUCTIVE CORRELATES OF ENVIRONMENTAL VARIATION AND NICHE EXPANSION IN THE CAVE SWALLOW IN TEXAS ---------- *Robert F. Martin* 506

HORNED LARK BREEDING BIOLOGY AT CAPE ST. MARY'S, NEWFOUNDLAND
Richard J. Cannings and William Threlfall 519

ASPECTS OF THE BREEDING BIOLOGY OF A SUBTROPICAL ORIOLE, *Icterus gularis*
Barbara Yohai Pleasants 531

GENERAL NOTES

AN EXAMPLE OF A HYBRID GREEN JAY × BLUE JAY
Warren M. Pulich and Rebecca M. Dellinger 538

DUSKY SEASIDE SPARROW FEEDS RED-WINGED BLACKBIRD FLEDGLINGS
James L. Rakestraw and James L. Baker 540

STATISTICAL SIGNIFICANCE AND DENSITY-DEPENDENT NEST PREDATION
Stephen D. Fretwell and Frank S. Shipley 541

A COMPARISON OF NEST-SITE AND PERCH-SITE VEGETATION STRUCTURE FOR SEVEN SPECIES OF WARBLERS ---------- *Scott L. Collins* 542

USE OF ARTIFICIAL PERCHES ON BURNED AND UNBURNED TALLGRASS PRAIRIE
Janet Jean Knodel-Montz 547

JUVENILE PEREGRINE FALCON SWOOPS ON ROSEATE SPOONBILLS ---------- *E. Scott Clark* 548

SYMBIOTIC INTERACTION BETWEEN STARLINGS AND DEER ---------- *Robert K. Murphy* 549

CATTLE EGRETS FEEDING IN ASSOCIATION WITH HUMAN WORKERS -------- *G. K. Menon* 549

SCRUB JAY CAPTURES HERMIT THRUSH IN FLIGHT
M. Robert McLandress and Ilse McLandress 550

FOOD HABITS OF BLACK-BELLIED WHISTLING DUCKS OCCUPYING RICE CULTURE HABITATS ---------- *Godfrey R. Bourne* 551

HOUSE SPARROWS FLUSHING PREY FROM TREES AND SHRUBS
Harland D. Guillory and Jack H. Deshotels 554

DIFFERENTIAL PREDATION BY TWO SPECIES OF PISCIVOROUS BIRDS
Fritz L. Knopf and Joseph L. Kennedy 554

RED PHALAROPE EATING CARRION ---------- *Wade Wander* 557

RE-MATING OF A LESSER SNOW GOOSE
Kenneth F. Abraham, Pierre Mineau and Fred Cooke 557

COMMON EIDER PLAYS "POSSUM" ---------- *Douglas B. McNair* 559

TERRITORIAL ATTACHMENT AND MATE FIDELITY BY HORNED GREBES
Robert S. Ferguson 560

EFFECTS OF REDHEAD NEST PARASITISM ON MALLARDS
Larry G. Talent, Gary L. Krapu and Robert L. Jarvis 562

SURVIVAL OF A DEMAXILLATE RED-WINGED BLACKBIRD ---------- *Kent L. Fiala* 563

MINIMIZING INVESTIGATOR DISTURBANCE IN OBSERVATIONAL STUDIES OF COLONIAL BIRDS: ACCESS TO BLINDS THROUGH TUNNELS
Gary W. Shugart, Mary A. Fitch and Vern M. Shugart 565

ORNITHOLOGICAL LITERATURE ---------- 570

PROCEEDINGS OF THE SIXTY-SECOND ANNUAL MEETING ---------- 575

INDEX ---------- 589

ACME
BOOKBINDING CO., INC.
SEP 9 1983
100 CAMBRIDGE STREET
CHARLESTOWN, MASS.

MCZ ERNST MAYR LIBRARY
3 2044 118 616 135